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Upscaling hypotheses on herbivore damage in plants facing environmental stress: Variation among scales and plant enemies in a relict tree

Adara Pardo*, Fernando Pulido

Institute for Dehesa Research-INDEHESA, University of Extremadura, Avenida Virgen del Puerto No. 2, 10600 Plasencia, Spain

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Abstract

The few existing analyses of broad-scale variation in plant–herbivore interactions are largely exploratory and not based on hypotheses on the effect of varying environmental conditions on the patterns of herbivore damage. However, there are two established hypotheses that relate herbivore damage and environmental stress mostly tested at the within-population level: the Plant Stress Hypothesis (PSH) and the Plant Vigor Hypothesis (PVH). To examine if support for the PSH holds true at broader scales, we tested it at the micro- (among individuals), meso- (between habitats) and macroscale (between geographical regions, Iberia and Macaronesia). We measured plant stress and leaf damage by different natural enemies (chewers, miners and pathogens) in 12 populations across the range of the relict tree *Prunus lusitanica*. Results regarding the proportion of leaves attacked by any enemy showed no support for the PSH at either micro or mesoscale, observing instead higher damage in less stressed individuals within populations and in high-quality habitats. However, the latter was true exclusively within the Macaronesian region, highlighting the important effect of the type of abiotic stress on plant susceptibility to herbivory. At the macroscale, alternatively, results showed support for the PSH: we observed a higher proportion of leaves attacked in Macaronesia than in Iberia, where plants unexpectedly exhibited greater stress symptoms. Among-scale inconsistencies may respond to the effect of distinct climatic factors governing both plant and herbivore dynamics at large scales, particularly in species with distributional ranges across contrasting climatic regions such as *P. lusitanica*. Finally, different plant enemies showed different patterns of damage, corroborating the need to study them separately to achieve consistent generalizations of these hypotheses.

Keywords: Herbivory; Multiple scales; Plant Stress Hypothesis; Plant Vigor Hypothesis; Relict flora

Introduction

Plant–herbivore interactions may vary among populations of a species due to plant or herbivore properties resulting in spatial differences in herbivore load and plant fitness (Hemmi & Jormalainen 2004). Damage levels may depend on the uneven effects of environmental conditions upon host plant susceptibility to herbivores (Garibaldi, Kitzberger, & Ruggiero 2011; Sopow, Bader, & Brockerhoff 2015). The existing analyses of broad-scale variation in herbivory have aimed at documenting regional clines in herbivore impact, tolerance or host preference (Alonso 1999; Connahs, Rodríguez-Castañeda, Walters, Walla, & Dyer 2009; Cornelissen & Stiling 2009; Garibaldi et al. 2011; Gaston, Genney, Thurlow, & Hartley 2004; Leimu, Riipi, &

*Corresponding author. Fax: +34 927425209.
E-mail address: adharapv@gmail.com (A. Pardo).

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Stærk 2005; Pennings et al., 2007; Sopow et al. 2015; Sotka & Hay 2002). However, these studies generally are exploratory and not based on hypotheses on the effect of varying environmental conditions on the regional pattern of herbivore load and damage, most likely due to a lack of a theoretical framework relating plant vigor and herbivore performance at broad scales. The term 'plant vigor' in this context is defined *sensu* Price's (1991) paper, as a high growth rate and the capacity to cope with environmental stress with few constraints on performance. Thus, we still lack a clear picture of how environmental stress, by altering plant vigor, influences herbivore distribution and damage at broader scales (but see Cobb et al. 1997). There are two established hypotheses relating herbivory damage and plant vigor, developed and mostly tested at the within-population scale. The Plant Stress Hypothesis (PSH) states that the impact of herbivores on plant fitness increases as plant stress increases due to reduced allocation to defences and/or increased nitrogen-related nutritional quality of plant tissues (Rhoades 1979; White 1969). A different view stems from the Plant Vigor Hypothesis (PVH), which states that herbivores should prefer more vigorous, fast-growing modules or individuals (Price 1991). The PVH does not provide any mechanistic explanation for the positive relationship between increased herbivore performance and plant vigor, but recognizes a number of possible drivers (*e.g.*, increased resources, higher food quality, lack of induced defensive compounds (Price 1991)). Although the PSH is widely cited, it is partly based on indirect evidence (Larsson 1989). Separate meta-analyses (Cornelissen, Fernandes, & Vasconcellos-Neto 2008; Huberty & Denno 2004; Koricheva, Larsson, & Haukioja 1998) have found very limited support for the PSH and a considerable explanatory success for the PVH. However, these two hypotheses may not be mutually exclusive (Price 1991): herbivores may perform better on stressed plants or populations, but within an individual plant, they may still prefer to feed on the most vigorous plant tissues (Cobb et al. 1997). Moreover, the importance of distinguishing among types and degrees of environmental stresses as well as types of natural enemies has been emphasized in order to make consistent predictions (Huberty & Denno 2004).

Indeed, plant natural enemies may exhibit differential responses to stress-mediated plant susceptibility. Price (1991) observed that 84% of all insects that prefer vigorous plants fed endophytically as galling or mining insects. In contrast, a meta-analysis found that gall-makers and chewing insects tend to support the PVH, whereas boring and sucking insects tend to support the PSH (Koricheva et al. 1998). There is still controversy as divergent results have been reported in different more recent studies; Huberty and Denno (2004) found that leaf chewers and miners showed inconsistent responses to water stress, whereas Cornelissen et al. (2008) showed that chewers and miners did increase in abundance on more vigorous plants. However, these latter results did not support a preference-performance linkage. With regards to pathogen behavior, generally, prolonged exposure of plants to abiotic stress conditions, such as drought or nutrient deprivation, results in the weakening of plant defences and enhanced susceptibility to pathogens (Boyer 1995; Desprez-Loustau, Marçais, Nageleisen, Piou, & Vannini 2006; La Porta et al. 2008). Although pathogens are theoretically expected to be negatively affected by water stress, as fungi require humid conditions for spore dispersal, germination and infection, indirect effects through host physiology may be predominant (Desprez-Loustau et al. 2006). In support of this line of evidence, a meta-analysis by Jactel et al. (2012) found that pathogens living on foliage caused more damage to water-stressed trees.

By up-scaling the PSH and PVH in a wider context, different expectations on the distribution of herbivore load and damage as a function of environmental stress can be derived. Thus, the impact of natural enemies should be more pronounced on stressed individuals within populations and in more stressful habitats and regions in agreement with the PSH. Alternatively, and consistent with the PVH, leaf damage should be more intense in vigorous individuals within populations and in less stressful habitats and regions. In this study, we examined if support for the PSH holds true at broader scales, testing it at the micro- (among individual trees within populations), meso- (between habitats) and macroscale (between geographical regions). Our study species, the relict tree *Prunus lusitanica* L., is considered to be a survivor of the laurel forests that inhabited the Mediterranean Basin during the Tertiary (Pignatti 1978). Specifically, we addressed the following questions: (1) Is leaf damage higher on more stressed individuals within populations as predicted by the PSH? (2) Is leaf damage higher in more stressful (low-quality) habitats as predicted by the PSH? (3) Is leaf damage higher in more stressful regions of the range as predicted by the PSH? (4) Are these responses similar for different plant natural enemies?

Materials and methods

Study species

The Portuguese laurelcherry (*P. lusitanica*) is an evergreen, lauroid tree, considered a paradigmatic example of a Tertiary relict tree persisting in the Mediterranean with scattered populations in Iberia, northern Morocco, and Macaronesia (Calleja, Benito-Garzón, & Sáinz Ollero 2009; Pulido, Valladares, Calleja, Moreno, & González-Bornay 2008). In Macaronesian populations, large trees (up to 20 m in height) grow in subtropical cloud forests, whereas Iberian populations comprise small and medium-sized trees growing in riparian sites surrounded by inhospitable dry habitats (Pulido et al. 2008). In both regions populations may be found under more or less stressful habitats according to water availability, topography, soil and wind conditions. *P. lusitanica* has the ability to synthesize, in addition to general defences commonly found in other woody plants such as phenolics, specific cyanogenic glycosides (prunasin and amygdalin), which may