

On global change, direct and indirect interactions, and
the structure of ecological communities: theoretical
and empirical tests

A Dissertation Presented for the
Doctor of Philosophy
Degree
The University of Tennessee, Knoxville

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December 2012

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To Emma and Noelia (sin ellas, nada de esto tendría sentido)
and to all who nurtured my curiosity and love for nature.

ACKNOWLEDGEMENTS

First and foremost, I would like to sincerely thank my doctoral advisor, Nathan Sanders, for his friendship, support and advice during all these years. Nate has been an excellent mentor, a great ecologist from whom to learn, and decent racquetball player but more importantly, he is an extraordinary person. I look forward to having him as a colleague and a friend throughout my ecological career and life.

I had the privilege to work with great people. I would like to give a special thanks to Dr. Daniel Simberloff for giving me the opportunity to work with him, and sharing his time along the way. It has being a great honor to have Dan as a committee member; he always provided a wealth of wisdom about ecology and the latest news from Argentina. I also thank my other committee members for their mentoring, Dr. James Fordyce and Dr. Michael McKinney.

I am deeply grateful to Noelia, my wife, my fiercest critic and my faithful field assistant always ready to go at 3:30 am to the field to check the marsupial's traps or to check on almost 2000 maqui fruits. Without her companion and help this wouldn't be possible. To my daughter, Emma, for bringing the perfect balance to my life.

Special thanks to Katie Stuble for her friendship, advice and hard work during my PhD. Katie has provided the encouragement and advice I needed during all these years. My other lab mates Lacy Chick, Melissa Burt, and Quentin Read who provide much needed comradeship in grad school. In particular, I am very grateful to two former members of the lab Gregory Crutsinger and Jean-Philippe Lessard for timeless hour of discussion about science and life. I am also grateful to Rob Dunn who allowed me to work with him and treated me like one of his own students.

I also thank the faculty, staff (especially Jaime Call) and grad students at the University of Tennessee, Knoxville - Department of Ecology and Evolutionary Biology.

I thank all the people that help me in the field for all their hard work in the USA and in Patagonia and for their thoughtful comments and suggestions, Guille Amico, Gonza Barrios, J.E. Canner Mili Chiessa, Maxi Gaetan, Juan Karlanian G.L. McCormick, Dorsi Morgan, Juan Paritsis and Rolo Vega. Thanks to Ezequiel Rodriguez-Cabal who is the author of the drawings in Chapter VII. I wish to thank J.K. Bailey, J.A. Schweitzer, J.J. Stachowicz, D. P. Vázquez , R. J. Warren II, T.J. Zelikova for providing comments and suggestions that greatly improved the chapters of this dissertation. Martin Nuñez a great friend that has been always there to talk about almost everything. I also would like to thank Romi Dimarco and Sara Kuebbing for all their friendship and support.

The administration of National Parks in Argentina and Historic Yates Mill County Park in North Carolina - USA for permission to carry research. Claudio Chehebar, Emilio Margarido, Tata Mujica, Mato Nuñez and Juan Santo at National Park Argentina provide excellent support for all my research in Patagonia.

This dissertation was supported by grants from the US National Science Foundation NSF DEB-1110431 and the Department of Ecology and Evolutionary Biology at the University of Tennessee.

Finally, I would like to thank my family for all their emotional, logistic support and for nurturing my curiosity and love for nature during all these years, Ricardo (papa), Cristina (mama), Miki, Eche, Edu, Lola, Gonza, Mari, Estefi y mis abuelos, Elsa, Yeya, Emilio y Hei. And to the argentinean that made us feel as we were at home, in Florida the Aguirre Family (Ignacio, Ana, Fran, Cata y Mateo), in Knoxville the Villarino Family (Nico, Fer, Agus, Vicky and Ana).

ABSTRACT

Human induced global change (climate change, CO₂ enrichment, nitrogen deposition, habitat degradation and biological invasions) is the most serious threat to biodiversity. Understanding how ecosystems will respond to different components of global change, and how these responses will affect key ecological processes, has become essential in contemporary ecology. For example, several studies have shown that exotic invasive species have negative impacts on the composition of communities, habitat structure and ecosystem processes.

Particularly, exotic species may have negative effects on species interactions due to local extinctions, competition and/or replacement of interactions. Despite the large body of research demonstrating the negative effects of exotic species on native communities, clear responses of the effect of invasive species on seed dispersal mutualisms are scarcely documented or have focused on only a relatively few invasive species. In this dissertation I used exotic species to (1) re-evaluate the inclusion of facilitation in niche theory, (2) study the establishment success and invasion rates of exotic species (i.e. tens rule), and (3) determine how exotic species has influenced community structure by altering the interaction between plants and animals, specifically, plant-seed dispersers mutualisms. In these studies, I established that interactions with exotic facilitators could increase the size of the realized niche by increasing the spatial distribution (reducing dispersal limitations), or by modifying the physical and chemical conditions of the

habitats, without altering the size of fundamental niche of native species. I found that the lack of information about failed species introductions and the tendency to report species that have become invasive more than those that have not results in an overestimation of establishment success and invasion rates. Additionally, I found that a suite of exotic vertebrate herbivores and exotic invertebrates lead to a cascade of linked extinctions by disrupting native plant-seed disperser mutualism. Together, my results highlight the negative effect of exotic invasive species and the importance of focusing on interactions among species to understand the causes and consequences of species loss from ecosystems.

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CHAPTER I. INTRODUCTION

Introduction

The rampant loss of biodiversity and the spread of invasive species are pervasive components of global change that threatens biodiversity (Wardle et al. 2011, Simberloff et al. in press). One of the greatest issues in contemporary ecology is to understand how the homogenization of biodiversity at all levels of organization and spatial scales will influence the assembly of communities and the functioning of ecosystems (Wardle et al. 2011). Yet, most conservation studies focus on either the importance of one or a few species or the relationship between some composite values, like species diversity and ecosystem functioning. In my dissertation, I used exotic species to (1) re-evaluate the inclusion of facilitation in niche theory, (2) study the establishment success and invasion rates of exotic species (i.e. tens rule), and (3) I seek to understand how the loss of some species and the gain of others influence interspecific interactions, such as mutualisms, the structure of communities, and ecosystem services.

Mutualisms are essential interactions not only for the persistence of mutualistic partners, but also for the maintenance of biodiversity and the integrity of ecosystems (Janzen 1980, Bond 1994, Levey and Benkman 1999, Herrera 2002). In particular, seed-dispersal mutualisms can influence seedling recruitment, the dynamics and persistence of populations, the distribution and abundance of species, plant community composition, and gene flow between populations (Howe and Smallwood 1982, Nathan and Muller-Landau 2000). The

disruption of seed dispersal mutualisms can affect the persistence of particular plant species and the structure of plant communities (Howe and Smallwood 1982, Wenny and Levey 1998, Jordano and Schupp 2000, Rodriguez-Cabal et al. 2007). Because many seed dispersal mutualisms often involve multiple dispersers, seed dispersal mutualisms may tend to be relatively resilient to changes in the identity of dispersing species (Bascompte et al. 2003). However, a growing number of studies have found that seed dispersal mutualisms are more specialized than they might at first appear (Ness et al. 2009, Gove et al. 2007).

The disruption of seed dispersal mutualisms could be more dramatic in communities with a high degree of asymmetry, that is, communities in which the majority of plants depend on only a few dispersers. The “keystone mutualist hypothesis” predicts that the disruption of a mutualism could trigger a cascade of linked extinction events throughout the rest of community (Gilbert 1980). Such consequences are a special case of the more general process of co-extinction, in which the loss or displacement of one species negatively affects the other species that depend upon it (Dunn et al. 2007, Dunn et al. 2009).

By preying on, competing with, and displacing native species, exotic species can dramatically reduce population sizes, which can ultimately result in local extinctions (Mack et al. 2000, Roemer et al. 2002). As a consequence, invasive animal species can affect seed dispersal mutualisms by consuming the reproductive parts of the plant (Kelly et al. 2006), or affecting populations of native dispersers (Christian 2001). Relatively few studies have addressed the

effects of exotic species on mutualisms (Traveset and Richardson 2006 and reference therein). Those that have tended to focus on the effects of exotic species on pollination mutualisms while the effects of invasive species on seed dispersal mutualism are rarely documented (Traveset and Richardson 2006) and have focused on only relatively few invasive species (Rodriguez-Cabal et al. 2009).

In my dissertation, I used observational, experimental, analytical and theoretical approaches to understand the effect of exotic invasive species on native ecosystems. In Chapter II, I review the inclusion of positive interactions in niche theory. Some studies have suggested that positive interactions can lead the realized niche of a species to be larger than its fundamental niche. I show that although positive interactions can counteract the effects of negative interactions and possibly modify the realized niche of a species, the realized niche of a species can never be larger than the fundamental niche. The results were reported in a paper in the journal *Ideas in Ecology and Evolution* in 2012.

In Chapter III, I show that the lack of information about failed species introductions and the tendency to report species that have become invasive more than those that have not result in an overestimation of the establishment success and invasion rates. The results of this short study were published in the journal *Diversity and Distributions* in 2009.

In Chapter IV, using data on the establishment success of two relatively very well-studied groups, the non-native birds in Hawaii and Britain, and comparing these data with those from a previous studies, I show that lack of

information about failed species introductions, and the tendency to report species that have become invasive more than those that have not, results in an overestimate of the establishment success and invasion rates of non-native species. The results of this study are reported in the journal *Biological Invasions* in 2012.

In Chapter V, I quantitatively review the available literature to determining the magnitude of the effect of the invasive Argentine ants (*Linepithema humile*) on seed-dispersal mutualisms. I found that the invasive Argentine ants have strong and largely negative effects on native seed dispersers, and as exotic ants do not replace native seed dispersers, potential shifts in diversity and change in ecosystem function may be a consequence. This study was published in the journal *Biology Letters* in 2009.

In Chapter VI, I used observational studies to quantify the impact of another invasive exotic ant, *Pachycondyla chinensis*, on seed dispersal mutualisms in its introduced range, the southeastern United States. I found that *P. chinensis* has a strong and negative effect on the abundance of the native seed dispersing ant, *Aphaenogaster rudis*, and because *P. chinensis* does not disperse seeds as effectively as *A. rudis*, the number of seed removed, and the number of myrmechochorous plants were lower in invaded than intact sites. This is the first study to document the consequences of the invasive ant *P. chinensis* on seed dispersal mutualism and its possible effects on myrmechochorous plant populations. The results were reported in a paper in the journal *Biological Invasions* in 2012.

Finally in Chapter VII, I used observational and experimental approaches to understand the effects of exotic ungulates and wasps on a unique keystone mutualism in the temperate forest of Patagonia-Argentina. This mutualism is comprised a hummingbird, a mistletoe, a marsupial, a bird and *Aristotelia chilensis*, the most common understory plant, which serves as the main host for the mistletoe. Reduction in abundance or distribution of any one of these species has the potential to significantly disturb the integrity of this south temperate forest. My results demonstrate that the loss of the host of keystone species, the mistletoe, disassembles the structure of a co-evolved interaction web. When the host is directly affected by the exotic herbivores and frugivore, there are indirect effects that lead to the local extinction of the mistletoe, the seed disperser (the marsupial and bird), and a pollinator (a hummingbird).

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CHAPTER II. POSITIVE INTERACTIONS IN ECOLOGY: FILLING THE FUNDAMENTAL NICHE

The Following section is a slightly modified version of a paper published in the journal *Ideas in Ecology and Evolution*:

Rodriguez-Cabal, M.A., Barrios-Garcia, M.N. and M.A. Nuñez. 2012. Positive interactions in ecology: filling the fundamental niche. *Ideas in Ecology and Evolution* 5: 36-41.

The use of “we” in this chapter refers to my co-authors and me. As the lead author of this article I was responsible for this paper. M.A.R.C. designed research, M.A.R.C., B.C.M.N. and M.A.N. wrote the paper.

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## **Abstract**

The role of negative interactions in shaping ecological communities and the realized niches of species has been a focus of considerable research for at least decades. Traditionally, the discrepancy between the size of the fundamental and realized niche of a species was attributed to the effect of negative interactions, such that the realized niche is always smaller than the fundamental niche. However, in the last decade, a series of studies have highlighted the important role that positive interactions played in shaping the structure of communities. This renewed interest in positive interactions has led to a reconsideration of the niche concept. Specifically, some investigators have suggested that positive interactions can lead the realized niche of a species to be larger than its fundamental niche. Here, we show that although positive interactions can counteract the effects of negative interactions and possibly modify the realized niche of a species, the realized niche of a species can never be larger than the fundamental niche.

## Introduction

The niche concept is an integral part of ecology, both currently and historically (Hardin 1960, Leibold 1995, Hubbell 2001, Chase and Leibold 2003, Levine and HilleRisLambers 2009, Pullian 2000, Vergnon et al. 2009, Chase and Myers 2011, Kylafis and Loreau 2011). However, the niche concept has been defined in several different ways, and remains one of the most confusing topics in ecology. Grinnell (1917) defined the niche as the place a species occupies in the environment. Elton's (1927) view of the niche differed from Grinnell's in that it focused on the functional role a species plays and its impact on the community. Both Grinnell's and Elton's niche definitions attributed niches to environments. Hutchinson (1957) instead attributed the niche to the species, and this definition is perhaps the most frequently used. Hutchinson (1957) defined the fundamental niche ( $\mathbf{N}$ ) as the sum of all  $\mathbf{X}_n$  variables, both physical and biological, required for a species ( $\mathbf{S}$ ) to persist. Moreover Hutchinson (1957) applied the Volterra-Gause principle (Gause 1934) to described the realized niche ( $\mathbf{N}'_1$ ) of a species ( $\mathbf{S}_1$ ) in the presence of another species ( $\mathbf{S}_2$ ) as the proportion of the fundamental niche of  $\mathbf{S}_1$  that is outside of the fundamental niche of  $\mathbf{S}_2$  ( $\mathbf{N}_1 - \mathbf{N}_2$ ), plus the intersection of both fundamental niches ( $\mathbf{N}_1 \cdot \mathbf{N}_2$ ) in which the birth rate of  $\mathbf{S}_1$  is equal to or greater than its death rate. Thus, ecologists generally credit the discrepancy between the size of the fundamental and the realized niches of a species to negative interactions such as competition (Fig II-1a).

Whereas the role of negative interactions in shaping natural communities has been the focus of ecological research (and heated debate) for decades (e.g. MacArthur 1958, Paine 1966, Janzen 1970, Tilman 1994), positive interactions were largely ignored until recently (e.g. Stachowicz 2001, Callaway et al. 2002, Bronstein et al. 2003, Bruno et al. 2003, Brooker et al. 2008, Van der Putten 2009). A positive interaction occurs when the presence of one species enhances the growth, survival, or reproduction of the interacting partner or neighbor but neither is negatively affected. In consequence positive interactions may have a strong influence on the spatial distribution of associated species over ecological (Choler et al. 2001) or evolutionary time scales (Valiente-Banuet et al. 2006). A series of studies on plant communities (e.g., Callaway 2007 and references there in) have highlighted the ubiquity of facilitation and its importance in shaping the structure of plant communities.

Bruno et al. (2003) further suggested that the inclusion of facilitation into niche theory leads to the paradox that the spatial extent of the realized niche can exceed the spatial range predicted by the fundamental niche (Fig II-1b). Bruno et al. (2003) went on to argue that by increasing the spatial extent of the distribution of a species, that species is thereby exposed to new conditions, and as such, the size of its realized niche has exceeded the size of its fundamental niche. But some empirical studies, such as Warren et al.'s (2010) work on ant-seed dispersal mutualisms clearly demonstrated that facilitation failed to expand the size of the realized niche of myrmecorous plant species over the fundamental niche of that same species. Here, we suggest that the size of the realized niche

cannot exceed the size of the fundamental niche, even though the spatial extent of the realized niche might indeed increase with positive interactions (Fig II-1c).

To support this contention, we offer five examples from the invasion biology literature. Invasive exotic species often become integrated into the recipient communities, disrupt their function and potentially create a new set of associations with native species (Richardson et al. 2000, Pearson and Callaway 2003, Aizen et al. 2008). However, in a small number of cases exotic species have facilitated a few native species via direct and indirect mechanisms (Vitousek et al. 1987, Vitousek and Walker 1989, Riera et al. 2002, Wonham et al. 2005, Pearson 2009). The consequences of facilitation by exotic invasive species include for example, geographical range expansion, changes in abiotic conditions or changes in food availability (Rodriguez 2006). In the following examples we show how the realized niche of native species has increased in the presence of exotic species without affecting the size of fundamental niche of the natives.

### **Lessons from exotic species**

In mutualistic interactions, such as plant-pollinator and plant-seed disperser interactions, the spatial distribution of one species is often limited by the extent of the interacting partner's distribution. For example, the introduction of exotic carnivore species in the Balearic Archipelago resulted in an increase in the distribution of the native shrub *Cneorum tricoccon* (Riera et al. 2002). Seeds of

these native shrubs were dispersed by native lizards in the genus *Podarcis*, which have become extinct following the introduction of several exotic carnivores. One of these exotic carnivore species, the pine marten (*Martes martes*), is also an important seed disperser. Records show that while native seed-dispersing lizards on the island of Majorca are restricted to low elevations (i.e., <500 m.a.s.l.), the current distribution of the plant extends up to 1000 m.a.s.l. Evidence based on seed dispersal experiments suggests that the exotic marten is responsible for the geographic range expansion of the native plant to high elevations. Thus, although the extent of the realized niche (i.e., increased elevation range) of these plants have increased following the introduction of the exotic species, the broad-scale geographic distribution of this plant group suggests that it is pre-adapted to these “new” abiotic conditions, which are included in its fundamental niche. Similarly, in a study of the seed dispersal interaction of the blood-root (*Sanguinaria canadensis*) by the red imported fire ant (hereafter RIFA; *Solenopsis invicta* Buren), Ness et al. (2004) found that RIFA affected seed destination by increasing dispersal toward forest edge ecotones, where native ant species rarely dispersed seeds. Thus, facilitative interactions between the exotic ant and the native plant led to a local increase in the spatial extent of bloodroot (e.g., number of patches occupied). An additional study with bloodroot showed that it can tolerate the physical conditions typical of forest gaps and can grow vigorously in light-rich habitats (Marino et al. 1997). Therefore, while bloodroot might be filling a greater portion of its fundamental

niche than before the introduction of RIFA, the range of the conditions that predicted its fundamental niche has not changed.

The spread of exotic species often results in physical alteration of existing habitats, which can include changes in abiotic conditions by creating new microhabitats. Such is the case of *Ficopomatus enigmaticus*, which is an invasive reef-building polychaete that creates new habitat for a number of native marine species. Schwindt and Iribarne (2000) found that many native species of crabs, amphipods and gastropods were more abundant beneath this reef-building polychaete than in uninvaded sites due to the introduction of novel physical structures that changes the abiotic conditions and providing refuge against predators. Similarly, the Asian hornsnail (*Batillaria attramentaria*), exotic to the Northwest Pacific coast of the United States, facilitates the establishment of native species, including two native hermit crabs (*Pagurus hirsutiusculus* and *P. granosimanus*), and exotic species (Wonham 2005). These species used the shell of the Asian hornsnail as substrate and refuge. However, these are examples of an invasive species increasing the realized niche of native species, because in these cases the exotic species are only providing additional microhabitat, not changing any condition of the native's fundamental niche.

Finally, various exotic plant species have a larger effect on nitrogen cycling on native ecosystems when they are associated with symbiotic nitrogen-fixer (Ehrenfeld 2003). One of the most dramatic examples comes from the work of Vitousek et al. (1987) and Vitousek and Walker (1989) on the invasion of *Morella faya* in Hawaii. *Morella faya* is a nitrogen-fixing invasive plant that

increases the N input into volcanic soils that are N-poor. Changes in N availability favor the subsequent establishment of native plants that are able to establish only in relatively fertile soils, and otherwise unable to establish in volcanic area. These increases in local distribution and number of individuals occurred without any reported effect on their tolerance to abiotic conditions (i.e., tolerance to soil with low levels of N). Therefore, these change only have an effect on the spatial distribution or abundances, and thus changing the realized niche of the native species without affecting any of the conditions that characterize their fundamental niche (Kearney 2006, Pullian 2000).

## **Discussion**

These examples show that interactions with exotic facilitators can increase the size of the realized niche by increasing the spatial distribution (reducing dispersal limitations), or by modifying the physical and chemical conditions of the habitats. However, whether the new range of conditions experienced by the benefiting species is greater than that predicted by the fundamental niche is uncertain because in most cases we do not even know what the fundamental niche is. Facilitation may lead to an increase in the size of the realized niche beyond that of the fundamental niche only if niche evolution occurs. However, niche evolution would only be possible if facilitative interactions were to create novel opportunities, such as those observed in several symbiotic associations. For example, the association between several vascular plants and fungi [i.e.,

mycorrhiza, (Wilkinson 2001)] and bacteria [i.e., *Rhizobia*, (Denison 2000)] has clearly contributed to the expansion of their geographic distribution over the fundamental niche of both species. Similar examples in which the fundamental niche of species has increased as a result of facilitation are the interaction of algae and fungi in lichens and the interaction between coral and zooxanthellae. Only in such cases, where neither of the species could persist in a new area without the other species, the realized niche occupied by the mutually obligate species is greater than the fundamental niche occupied by each species in isolation from the other.

We consider that since Hutchinson (1957) emphasized the role of interspecific competition to describe the realized niche, negative interactions had become the core of niche theory for over 50 years. A clear example is Austin (1999), who described the fundamental niche of a species as its distribution in the absence of interspecific competition, and the realized niche as the species distribution following competition and other biotic interactions. Consequently, if the fundamental niche were defined only as the physical requirements of the species, the realized niche of the species would be greater than its fundamental niche in the presence of only positive interactions [Bruno et al. (2003) paradox]. However, Hutchinson's definition of the fundamental niche included all physical and biological requirements for the species to persist (Hutchinson 1957; p. 416). Here, we are not suggesting that the inclusion of facilitation to niche theory as proposed by Bruno et al. (2003) is incorrect. The accomplishment of Bruno et al. (2003) in incorporating positive interactions into ecological theory is outstanding

and beyond debate. What we are suggesting is that facilitation can, and certainly do, contribute to mitigate negative interactions, but facilitation cannot cause the expansion of the realized niche over the fundamental niche. We nevertheless show that positive interactions may allow a greater filling of the fundamental niche of a species. Thus the inclusion of facilitation into niche theory may be better characterized as the processes, both physical and/or biological, that can expand the n-dimensional hypervolume of the realized niche that meets the requirements of the fundamental niche and can alleviate the effects of negative interactions and abiotic stress.

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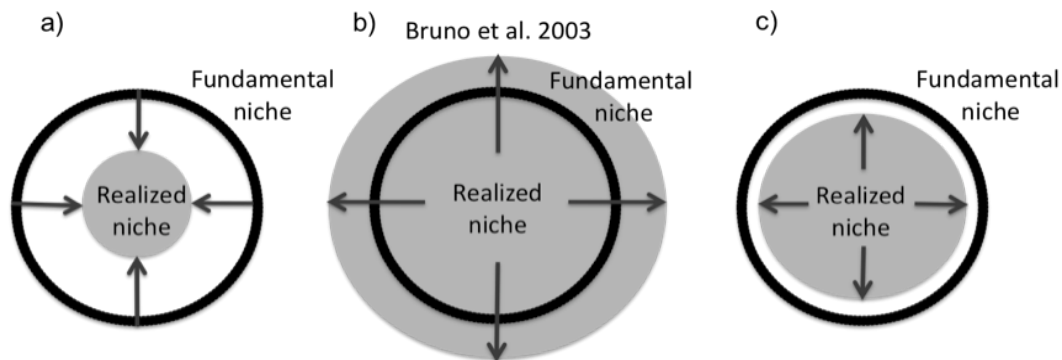


**Figure II-1.** Three different niche concepts. a) Hutchinson (1957)'s niche concept, the realized niche (grey circle) is the part of fundamental niche (black line) occupied by a species after accounting for negative interspecific interactions (such as predation, competition and parasitism). b) Bruno et al. (2003) niche concept, when facilitation is considered the realized niche (grey circle) can be larger than the fundamental niche (black line). c) Our hypothesis, that facilitation can mitigate the effects of negative interactions and expand the realized niche (grey circle) which is larger in (c) than in (a) but cannot overcome the fundamental niche (black line).

**CHAPTER III. ACROSS ISLAND AND CONTINENTS, MAMMALS  
ARE MORE SUCCESSFUL INVADERS THAN BIRDS**

The Following section is a slightly modified version of a paper published in the journal *Diversity and Distributions*:

Rodriguez-Cabal, M.A., Barrios-Garcia, M.N. and Simberloff, D. 2009. Across island and continents, mammals are more successful invaders than birds (Reply). *Diversity and Distributions* 15: 911-912.

The use of “we” in this chapter refers to my co-authors and me. As the lead author of this article I was responsible for this paper. M.A.R.C., B.C.M.N. and D.S. designed research and wrote the paper.

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Abstract

The aim of this manuscript is to show that the lack of information about failed species introductions and the tendency to report species that have become invasive more than those that have not result in an overestimation of the establishment success and invasion rates by Jeschke (2008). Remarkably, Jeschke (2008) notes that the actual numbers of introduced species are unknown but states that this lack of knowledge does not affect his conclusion.

Introduction

The tens rule predicts that about 10% of all introduced species establish and about 10% of established species become invasive (Williamson and Brown 1986). This was an empirical rule, based on a few data sets, and to date no theoretical basis has been proposed. Jeschke (2008) found that mammals and birds have a much higher establishment success rate and invasion probability than predicted by the tens rule. In his study, the average percentages of introduced mammals and birds that have established across continents and islands are 79% and 50%, respectively, and 63% of the mammals and 34% of the birds established became invasive (see Figure 1 in Jeschke 2008). In addition, his study does not support the hypothesis that islands are more susceptible to invasion than continents.

In his paper Jeschke calculated establishment success as the fraction of introduced species that have become established, and invasion success as the fraction of established species that have spread substantially from their points of introduction. As was pointed out by Simberloff (1995, misquoted in Jeschke 2008), data are inadequate to draw strong conclusions about the tens rule or invasibility of island and continents. For instance, the chance of an exotic species arriving in a new area increases greatly with the presence of or proximity to ports, airports, mail centres, and road and rail crossings (Mack et al. 2000, Floerl and Inglis, 2005, Ward et al. 2006). In a Postnote published by The Parliamentary Office of Science and Technology of United Kingdom (2008), the government of

the United Kingdom states "...The Plant Health and Seeds Inspectorate is responsible for inspecting relevant products entering England and Wales for non-native pests and diseases. There is a lack of systematic surveys, so the presence of other types of non-native species is usually detected in surveys undertaken for other purposes..." Additionally, Work et al. (2005) examined several types of cargo traversing the USA-Mexico border and found that only between 19-50% of insects are detected in inspections carried out for this purpose.

The lack of information about the frequency of different types of introductions and number of failed introductions means that Jeschke (2008) surely overestimated establishment success rate. A large fraction of the unsuccessful invasions are never reported, and without these data the values reported by Jeschke (2008) are biased. Remarkably, Jeschke (2008) notes that the actual numbers of introduced species are unknown but states that this lack of knowledge does not affect his conclusion. In a previous paper, Jeschke and Strayer (2005) directly addressed the fact that failures are less likely to be recorded than successes. For mammals and birds, in many regions (e.g., North America and Europe), established introduced species are probably quite well known, so that the percentages Jeschke (2008) reports for fraction of established introductions that become invasive is probably fairly accurate. This would not be the case with insects or plants, and it might not be the case for birds or mammals of less well-studied regions. Since species that have become invasive would be

more likely to be reported than those that have not, any inaccuracy would be in the direction of overestimating the fraction that become invasive.

Discussion

In conclusion, Jeschke (2008) probably overestimates the fraction of introduced species that have become established and the fraction of these that have become invasive. Ultimately, his conclusion that islands are not more susceptible to invasion than continents is misleading. His analyses also do not control for propagule pressure, which plays a key role in determining whether an introduced species establishes and spreads. This role cannot simply be ignored because of absence of data (see Sol et al. 2008).

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CHAPTER IV. OVERESTIMATION OF ESTABLISHMENT SUCCESS OF NON-NATIVE BIRDS IN HAWAII AND BRITAIN

The Following section is a slightly modified version of a paper published in the journal *Biological Invasions*:

Rodriguez-Cabal, M.A., Williamson, M. and D. Simberloff. (In press). The establishment success of non-native birds in Hawaii and Britain. *Biological Invasions* DOI 10.1007/s10530-012-0285-y

The use of “we” in this chapter refers to my co-authors and me. As the lead author of this article I was responsible for this paper. M.A.R.C., M.W and D.S. designed research, analyzed data and wrote the paper.

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## **Abstract**

The tens rule states that 10% of all introduced species establish and about 10% of those species become invasive. Several studies have failed to support the tens rule. However, these studies are beset by a general weakness: many unsuccessful invasions are never reported, and without these data tests of the tens rule are inadequate. Here, using data on the establishment success of non-native birds in Hawaii and Britain and comparing these data with those from a previous study, we show that lack of information about failed species introductions, and the tendency to report species that have become invasive more than those that have not, result in an overestimate of the establishment success and invasion rates of non-native species.

## Introduction

In order to become invasive, a non-native species must pass through three stages: arriving in a new region, establishing a population, and spreading. Of the many species introduced accidentally or intentionally to new regions, the majority fail to establish and an even smaller proportion become invasive (Williamson and Brown 1986). In an attempt to quantify the probability of getting from initial introduction to invasion, Williamson and Brown (1986) formulated the tens rule, which states that about 10% of all introduced species establish and about 10% of established species become invasive, with limits between about 5 to 20% at each step (Williamson 1993). However, the tens rule has no theoretical basis; it does not explain or predict. It is just a descriptive pattern.

Recent reviews have challenged the tens rule (Jeschke and Strayer 2005, Jeschke 2008). Jeschke and Strayer (2005) found that establishment success rates of freshwater fish, mammals, and birds native to Europe and introduced to North America, or vice-versa, were almost 50% in each direction, and almost 50% of these species became invasive (see Figure 2 in Jeschke and Strayer 2005). Similarly, Jeschke (2008) reported that 79% and 50% of introduced mammals and birds, respectively, established at the site of introduction and 63% of the mammals and 34% of the birds that established became invasive (see Figure 1 in Jeschke 2008).

One problem with such studies is that the data are inadequate to draw conclusions about the tens rule (Simberloff 1995, Rodriguez-Cabal et al. 2009),

because failures are less likely to be recorded than successes. Although Jeschke and Strayer (2005) noted this problem and conceded that this can render some of their estimates of establishment success too high, Jeschke (2008) felt that the lack of knowledge of unsuccessful introduced species would not affect his conclusion. Rodriguez-Cabal et al. (2009) demurred, but Jeschke (2009), in reply, argued that his conclusion in 2008 was based on careful analysis of two taxa, mammals and birds, that are so well-studied that knowledge gaps are not debilitating. Here we examine the conclusions of Jeschke (2008, 2009) by analyzing data on the introduction of land birds in Hawaii and Britain, part of the same data analyzed by Jeschke (2008), and giving details of the best figures we have been able to obtain for introduction and establishment of non-native bird species in these archipelagos.

## **Material and methods**

We reviewed literature on the number of non-native bird species introduced and those that have established self-sustaining populations in the Hawaiian and Britain archipelagos. We considered a species as established when the population has persisted for at least 15 years. We did not include species for which it was known that only one individual was released. Then we compared our data to those of Jeschke (2008). Jeschke (2008) did not report data for Ni'ihau, Kaho'olawe and Hawai'i. Although data are available for these, we

present data for only those Hawaiian islands reported by Jeschke (2008) in our Tables; the full data are in the Appendix.

### **Data**

The data from the Hawaiian Islands were collected from an exhaustive bibliography review of 71 years of the journal Elepaio from its first issue to the November 2010 issue (volume 70, number 8). Additional information on the Hawaiian archipelago was extracted from a recent review of the bird fauna of Hawaii by Pyle and Pyle (2009) (Appendix A). The only fully reliable list of British birds and their status is the British List maintained by the British Ornithologists' Union (BOU), reviewed annually, and available at <http://www.bou.org.uk/thebritishlist/British-List-2010.pdf>. It has six sections, categories, A-F. Category A is "Species recorded in an apparently natural state at least once since 1 January 1950," so it includes regular and irregular breeders, migrants and natural stragglers. Category C is introduced bird species with self-sustaining populations. The BOU requires much detailed evidence before accepting a population as self-sustaining. The detailed procedures used by the BOU before accepting a species as C (established) are fully described in Dudley (2005) and the papers he quotes. Category E is "introductions, human-assisted transportees or escapees from captivity" but "thought not to be self-sustaining." It is "provisional" and "not exhaustive." For invasion biologists, species in E are casual and most of those in C are established (naturalized). However, Category C has been split since 2005 into six subcategories (Dudley 2005). For our

purpose, established introduced species are those in C1 (straight introductions), C2 (as C1 but also in A) and C4 (feral), totalling 18 allowing for double entries. Casual species are those in E but not also in A or C. Our count is 288 in E less 29 also in A or C, which gives 259 casuals. Data were analyzed using a Chi-square test on the number of casual (introduced minus established) vs established species.

## **Results and discussion**

We found that, of the seven islands analysed by Jeschke (2008), five have lower proportions of established birds than he reported, two of them significantly so, and two have higher proportions (Table IV-1). For the Hawaiian archipelago and Britain, the numbers of events recorded by Jeschke (2008) were too low, approximately by half for the Hawaiian archipelago and almost nine times smaller for Britain. These results show that his test of the tens rule is inadequate because the data he used are insufficient. For the Hawaiian archipelago he used Simberloff and Boecklen (1991) for O'ahu, Moloka'i, Lana'i and Mau'i, Case (1996) for Kauai, and Sol et al. (2000) for the Hawaiian archipelago. For Britain, he used Case (1996), who in turn used three sources, Heinzel et al. (1972), Lever (1987), and Ridpath and Moreau (1966). Heinzel et al. (1972) is a field guide with a very short list of casuals and is not concerned with introduced status. Lever (1987) is a good natural history book but not systematic and scarcely treats casuals, while Ridpath and Moreau (1966) is on the birds of

Tasmania. Jeschke (2008) also used Williamson and Brown (1996), though his figures are not those given there. Additionally, even though we used two of the most up-to-date and well-recorded data sets, these data sets are far from exhaustive. We believe that our proportions are still too high, because species that have spread from their introduction location would be more likely to be reported than those that have not, and any inaccuracy would thus be in the direction of overestimating the fraction of non-native species that became established. We also believe that our conclusions are also valid for mainland ecosystems. Moreover, Britain is a continental island and, for birds, behaves like a mainland system. Finally, from our results we can expect the bias to be higher for taxa for which information on introduction attempts is more incomplete.

In conclusion, that the tens rule frequently does not always hold is scarcely news. In Fig 2.2 in chapter 2 of Williamson (1996), 50% of the points, including all the Hawaiian data points, are outside the 5-20% limits that Williamson (1993) suggested as a rough rule, not generating precise descriptions (Williamson 1996, 2006). We still feel that the tens rule is a helpful concept that can be used as a point of reference.

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**Table IV-1. Number of introduced and established non-native birds.**

Comparison between the number of introduced and established non-native birds, and the proportion of success, in the Hawaiian islands and Britain in this study and in Jeschke (2008). Additionally, we added data on all non-native birds introduced into the Hawaiian archipelago. Significant *P*-values are indicated by \*.

|                      |                                 | Our data |         |    | Jeschke (2008) |         |    | $\chi^2$ | <i>P</i> |
|----------------------|---------------------------------|----------|---------|----|----------------|---------|----|----------|----------|
|                      |                                 | Introd   | Establi | %  | Introd         | Establi | %  |          |          |
| Kaua'i               | Total                           | 70       | 37      | 53 | 52             | 27      | 52 | 0.002    | 0.961    |
| O'ahu                | Columbiformes and Passeriformes | 64       | 28      | 44 | 53             | 31      | 58 | 2.272    | 0.132    |
|                      | Total                           | 118      | 41      | 35 |                |         |    |          |          |
| Moloka'i             | Columbiformes and Passeriformes | 23       | 20      | 87 | 18             | 16      | 89 | 0.035    | 0.851    |
|                      | Total                           | 41       | 31      | 73 |                |         |    |          |          |
| Lana'i               | Columbiformes and Passeriformes | 24       | 18      | 75 | 18             | 13      | 72 | 0.015    | 0.903    |
|                      | Total                           | 41       | 30      | 73 |                |         |    |          |          |
| Mau'i                | Columbiformes and Passeriformes | 30       | 22      | 73 | 28             | 18      | 64 | 0.554    | 0.457    |
|                      | Total                           | 67       | 35      | 52 |                |         |    |          |          |
| Hawaiian archipelago | Total                           | 183      | 57      | 31 | 103            | 45      | 44 | 5.092    | 0.024*   |
| Britain              |                                 |          |         |    |                |         |    | 18.63    |          |
|                      | Total                           | 277      | 18      | 6  | 30             | 9       | 30 | 9        | <0.001*  |

**CHAPTER V. QUANTITATIVE ANALYSIS OF THE EFFECTS OF  
THE EXOTIC ARGENTINE ANT ON SEED DISPERSAL  
MUTUALISMS**

The Following section is a slightly modified version of a paper published in the journal *Biology Letters*:

Rodriguez-Cabal, M.A., Stuble, K.L., Nunez, M.A. and N.J. Sanders. 2009.  
Quantitative analysis of the effects of the exotic Argentine ant on seed-dispersal mutualisms. *Biology Letters* 5: 499-502.

The use of “we” in this chapter refers to my co-authors and me. As the lead author of this article I was responsible for this paper. M.A.R.C., S.K.L. and N.J.S. designed research, M.A.R.C. analyzed data and M.A.R.C., S.K.L., M.A.N. and N.J.S. wrote the paper.

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Abstract

Although it is increasingly clear that exotic invasive species affect seed dispersal mutualisms, a synthetic examination of the effect of exotic invasive species on seed dispersal mutualisms is lacking. Here, we review the impacts of the invasive Argentine ant (*Linepithema humile*) on seed dispersal. We found that sites with *L. humile* had 92% fewer native ant seed dispersers than did sites where *L. humile* was absent. In addition, *L. humile* did not replace native seed dispersers; as rates of seed removal and seedling establishment were all lower in the presence of *L. humile* than in its absence. We conclude that potential shifts in plant diversity and concomitant changes in ecosystem function may be a consequence of Argentine ant invasions, as well as invasions by other ant species. Because very few studies have examined the effects of non-ant invasive species on seed dispersal mutualisms, the prevalence of disruption of seed-dispersal mutualisms by invasive species is unclear.

Introduction

Seed dispersal mutualisms influence seedling recruitment, population dynamics, species distributions, plant-community composition, and gene flow (Howe and Smallwood 1982, Nathan and Muller-Landau 2000). However, the spread of exotic invasive species (invasive species hereafter) threatens seed dispersal mutualisms, with potential consequences for native populations and communities (Traveset and Richardson 2006, Tylianakis et al. 2008).

Although a growing number of studies have examined whether invasive species disrupt seed dispersal mutualisms, either by affecting the dispersal agent or the plant (e.g., Bond and Slingsby 1984, Kelly et al. 2006), a quantitative examination of the effect of invasive species on seed dispersal mutualisms is lacking (Traveset and Richardson 2006). Here, we report the results of a meta-analysis aimed at determining the magnitude of the effect of the invasive Argentine ants (*Linepithema humile*) on seed-dispersal mutualisms. *L. humile* has become established in Mediterranean climates globally. Importantly, some of these regions are biodiversity hotspots and harbor a number of unique and endemic plant species, which may rely on native ants to disperse their seeds. Seed dispersal by ants (i.e., myrmecochory) is particularly important in that it involves hundreds of ant species and thousands of plant species across many terrestrial ecosystems (Beattie and Hughes 2002, Rico-Gray and Oliveira 2007). Our focus is on the invasive Argentine ant, a species known to have dramatic effects on native communities and ecosystems (Holway et al. 2002). Specifically,

we ask three questions: (1) Do Argentine ants reduce the abundance of seed dispersers? (2) Do invasive Argentine ants disrupt seed dispersal mutualisms by reducing the number of seeds removed? And (3) Do Argentine ants reduce seedling recruitment?

Material and methods

On 31 January, 2009, we searched Web of Science to locate publications that included the keywords “disr* seed dispersal”, “predation seed disper*”, “competition seed disper*”, “disrup* mutualis*” and “inva* or introduced or alien or exotic or non-native or non-indigenous.” We also used our knowledge of the literature and scanned the references of any relevant papers to obtain additional sources from the primary literature. To be included in our meta-analysis, a study had to be either an observational or experimental study on seed dispersal in both the presence and absence of an invasive species in the same area.

In total, we found 14 publications focusing on 31 plant species that met our criteria. Eleven out of the fourteen articles focused on the impact of invasive ants on seed dispersal mutualisms, and of these eleven; ten were concerned with the effect of *L. humile* and one with the effect of *Solenopsis invicta*. Because of the low number of publications dealing with species other than *L. humile* we report only the results of a meta-analysis quantifying the effect of this species on seed dispersal mutualisms.

Nine of the ten publications used in the meta-analysis examined seed removal, three examined seedling establishment, and four examined the abundance of seed dispersers (Appendix A). From each of these publications, we extracted quantitative estimates of the mean number of seeds removed, seedlings established, and/or seed dispersers in the presence and absence of the invasive species. Several publications contained information for more than one plant species or seed dispersal agent, in which case we treated each as distinct data points in our analyses if the species were analyzed separately by the author(s) of the original study. If the data were not available in the text, table, or online appendix, we used GetData Graph Digitizer (v. 2.22, copyright S. Fedorov, 2002-2006) to extract data from figures in the original manuscript.

We calculated the effect of invasive species on seed dispersal mutualisms (effect size) as the log-response ratio ($\ln R$),

$$\ln R = \ln \left(\frac{\bar{X}_P}{\bar{X}_A} \right)$$

where $\bar{X}_P$ is the mean of the response variable in the presence of the invasive species and $\bar{X}_A$ is the mean of the response in the absence of the invasive species (Hedges et al. 1999, Osenberg et al. 1999). A negative effect size indicates that the invasive species reduced the number of seeds removed, seedlings established, or seed dispersers. We performed a meta-analysis using a random effect model and calculated the weighted mean effect size and 95% bootstrap CI for the four response variables using MetaWin (Rosenberg et al. 2000).

Results and discussion

Invasive species can affect diversity, modify ecosystem function, and alter interactions among native species (Mack et al. 2000, Traveset and Richardson 2006, Tylianakis et al. 2008). In our study, sites with *L. humile* contained 92% fewer native seed dispersers than did sites without *L. humile* (Fig V-2). Moreover, it seems unlikely that *L. humile* replaces native seed dispersers, as overall rates of seed removal and seedling establishment were lower in the presence of invasive ants than in their absence: sites with *L. humile* had, on average, 47% fewer seeds removed and seedling establishment was 76% lower, than when *L. humile* was present (Fig V-2).

Our quantitative analysis supports previous studies that have documented the effects of invasive ants on seed dispersal mutualisms (Holway et al. 2002, Ness and Bronstein 2004). Indeed, our study suggests that the major impact of invasive Argentine ants results from their dramatic reduction of the abundance of native seed-dispersing ants (Fig V-2). This is not surprising, as Argentine ants clearly alter the composition of native ant communities (Christian 2001, Carney et al. 2003, Gómez et al. 2003, Gómez and Oliveras 2003, Rowles and O'Dowd 2007).

Seed dispersal by ants has been hypothesized to benefit plants by reducing competition and predation, minimizing the effects of fire, and depositing seeds in nutrient-rich sites (Bond and Slingsby 1984, Christian 2001, Ness and Bronstein 2004). Plants that depend on ants as seed dispersers often

disproportionately rely on a single ant species (Gove et al. 2007), making them especially vulnerable if the behaviour or abundance of the keystone mutualist is altered (Giladi 2006). Our meta-analysis and the studies that did not meet our criteria for inclusion in the meta-analysis suggest that invasive ants, such as *L. humile* and *S. invicta*, are typically poor seed dispersers relative to the native ants they displace. Invasive ants may find seeds more slowly or collect fewer seeds per unit of time than do natives (Horvitz and Schmske 1986, Bond and Slingsby 1984, Carney et al. 2003, Gómez et al. 2003, Ness 2004, Oliveras et al. 2007, Rowles and O'Dowd 2009). Additionally, invasive ants often bury seeds less frequently than do native ant species (Bond and Slingsby 1984, Christian 2001, Zettler et al. 2001, Gómez et al. 2003, Gómez and Oliveras 2003). These invasive ants may also act as seed predators (Horvitz and Schmske 1986, Zettler et al. 2001) or consume elaiosomes without moving seeds (Quilichini and Debussche 2000, Gómez et al. 2003, Ness 2004). However, it is important to note that native ants may also consume seeds and the relative importance of seed predation among native ants may influence the ultimate impact of invasive ants.

Body size in ants plays a crucial role in seed dispersal (Ness and Bronstein 2004), an important fact, as invasive ants are sometimes smaller than the native species that they exclude (McGlynn 1999, Holway et al. 2002). As a result, invasive ants frequently fail to disperse large elaiosome-bearing seeds while readily dispersing small native and exotic seeds (Ness 2004, Witt et al. 2004, Rowles and O'Dowd 2009). However, the ultimate impact of Argentine ants

on seed dispersal in a community may be mediated by seed size. For example, Rowles and O'Dowd (2009) showed that Argentine ants removed large as well as small diaspores but this was influenced by elaiosome mass. Additionally, when they do remove seeds, dispersal distances by invasive ants are often shorter than those of native species (Horvitz and Schemske 1986, Bond and Slingsby 1984, Ness 2004, Rowles and O'Dowd 2009). Finally, not only do invasive ants disrupt seed-dispersal mutualisms between native species but also they successfully disperse seeds of exotic plants (Rowles and O'Dowd 2009).

As with any meta-analysis, our results could be biased by that the failure to publish studies that show no effects of invasive species. In addition, there may be a research bias, whereby researchers tend to study sites or species (such as *L. humile*) where effects are likely to be found. We would encourage publication of any results showing non-negative effects of invasive ants on seed dispersal mutualisms.

Finally, we would like to highlight the fact that we found few studies on species other than *Linepithema humile*. In our opinion, this paucity of studies suggests a clear need for ecologists to examine the effects of invasive species on seed dispersal mutualisms. We also suggest that long-term studies are needed to understand the population-level consequences of the disruption of seed dispersal mutualisms by invasive species. Nevertheless, our results at least suggest that Argentine ants have strong negative effects on the dispersal of seeds and the establishment of seedlings, but it is unclear how these effects

influence population dynamics of native plant species, or the structure of native plant communities.

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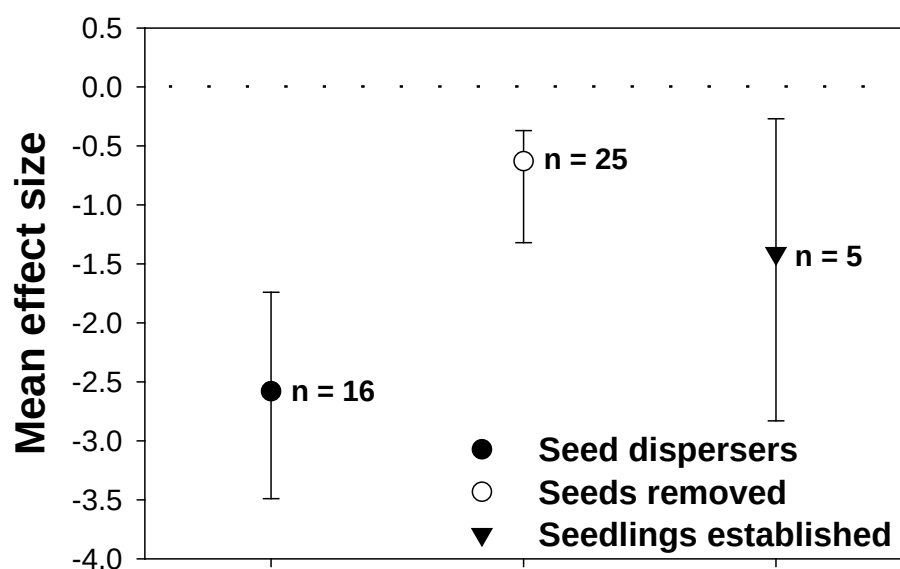


Figure V-2. Results from the meta-analysis showing the negative effects of the exotic ant *Linepithema humile* on native plant-seed dispersal mutualisms. We calculated the effect size using the log response ratio of number of seed dispersers, seeds removed and seedlings established. Symbols represent the mean effect size $\pm$ 95% CI's. If the CI's do not overlap the horizontal line at 0, then there is a significant negative effect of the presence of Argentine ants on that aspect of seed dispersal.

**CHAPTER VI DISRUPTION OF ANT-SEED DISPERSAL
MUTUALISMS BY THE INVASIVE ASIAN NEEDLE ANT
(*PACHYCONDYLA CHINENSIS*)**

The Following section is a slightly modified version of a paper published in the journal *Biological Invasions*:

Rodriguez-Cabal, M.A., Stuble, K.L., Guénard, B., Dunn, R.R. and N.J. Sanders. 2012. Disruption of ant-seed dispersal mutualisms by the invasive Asian needle ant (*Pachycondyla chinensis*). *Biological Invasions* 14: 557-565.

The use of “we” in this chapter refers to my co-authors and me. As the lead author of this article I was responsible for this paper. M.A.R.C., R.R.D., N.J.S. designed research, M.A.R.C. and S.K.L. performed research, M.A.R.C. analyzed data and M.A.R.C., S.K.L., G.B., R.R.D., and N.J.S. wrote the paper.

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## Abstract

By disrupting the structure of native ant assemblages or affecting particularly important species, invasive ants can have effects across trophic levels. Most studies to date, however, have focused on the impacts of two invasive ant species (*Linepithema humile* and *Solenopsis invicta*). The impacts of many other invasive ant species, such as *Pachycondyla chinensis*, on ecological processes in their introduced range are unknown. In this study we tested the hypothesis that *P. chinensis* disrupts ant-seed dispersal mutualisms by displacing native ant species, especially the keystone mutualist *Aphaenogaster rudis*, while failing to disperse seeds itself. The number of *A. rudis* workers was 96% lower in invaded than in intact plots, and the number of seeds removed was 70% lower in invaded than in intact plots. Finally, in invaded plots the abundance of *Hexastylis arifolia*, a locally abundant myrmecochorous plant, was 50% lower than in plots where *P. chinensis* was absent. The most parsimonious interpretation of our results is that *P. chinensis* causes precipitous declines in the abundance of *A. rudis* within invaded communities, thereby disrupting the ant-plant seed dispersal mutualism and reducing abundances of ant-dispersed plants. In sum, the magnitude of the effects of *P. chinensis* on seed dispersal are quantitatively similar to those documented for the intensively studied invasive Argentine ant. We suggest that more studies on the impacts of less-studied invasive ant species on seed dispersal mutualisms may increase our knowledge of the effects of these invaders on the functioning of ecosystems.

## Introduction

Though local communities often include many species, those species are not necessarily equal in their effects on one another. In many cases, a single species can have disproportionate effects on other species and on ecosystem processes (Ellison et al. 2005). Invasive species provide many key examples of the strong effects of single species ramifying through communities and ecosystems. For example, the presence of invasive plant species can alter fire regimes (D'Antonio and Vitousek 1992), nutrient cycling (Vitousek 1990, Tardiff and Stanford 1998), and other ecosystem processes (Levine et al. 2003). The arrival of some invasive species can also disrupt mutualistic interactions such as pollination (Vazquez and Simberloff 2004) or seed dispersal (Traveset and Richardson 2006, Rodriguez-Cabal et al. 2009). Such effects arise, at least in part, because of reductions in the abundance or alterations of the behavior of one or a few native species (Traveset and Richardson 2006, Rodriguez-Cabal et al. 2009).

The disruption of seed dispersal mutualisms can affect the persistence of particular plant species and the structure of plant communities (Howe and Smallwood 1982, Schupp and Fuentes 1995, Wenny and Levey 1998, Jordano and Schupp 2000, Rodriguez-Cabal et al. 2007). On the one hand, because many seed dispersal mutualisms involve many or at least multiple dispersers, seed dispersal mutualisms may tend to be relatively resilient to changes in the identity of dispersing species (Vazquez and Aizen 2004, Vazquez et al. 2005, Bascompte et al. 2003, 2006). On the other hand, however, a growing number of

studies have found that seed dispersal mutualisms are more specialized than they appear (Gilbert 1980, Gove et al. 2007, McCoy 2009). In such specialized systems, the impact of invasive species on seed dispersal mutualisms might be especially pronounced.

Invasions by ant species represent an interesting context in which to examine the dependence of seed dispersal on individual species. Studies on Argentine ants (*Linepithema humile*) and red imported fire ants (*Solenopsis invicta*) generally indicate strong negative effects on seed dispersal mutualisms. After displacing populations of native seed dispersers, *L. humile* and *S. invicta* often fail to disperse seeds effectively (Bond and Slingsby 1984, Gómez and Oliveras 2003, Gómez et al. 2003, Ness 2004, Carney et al. 2003, but see Stuble et al. 2010). The majority of studies of the impacts of invasive ants on seed dispersal have focused on these two ant species (Holway et al. 2002, Ness and Bronstein 2004, Rodriguez-Cabal et al. 2009), though many other introduced ant species are sufficiently abundant to compete with native ants for resources such as seeds (Holway et al. 2002), and even more introduced species could potentially be considered as invasive in the future (McGlynn 1999). Clearly, much remains to be learned about the potential impacts of other invasive ant species on seed dispersal mutualisms.

*Pachycondyla chinensis* (Emery) (Formicidae: Ponerinae) is an invasive ant whose abundance has recently been shown to be associated with dramatic changes in ant community composition in parts of its introduced range (Guénard and Dunn 2010). *P. chinensis* reduces the abundances of most native ant

species, including the important seed disperser *Aphaenogaster rudis* (which is part of a species complex, but will be referred to as *A. rudis* here), while apparently having either no or positive effects on the larger-bodied species in the genera *Camponotus* and *Formica* (Guénard and Dunn 2010). In the temperate deciduous forests of eastern North America, *A. rudis* is responsible for between 48-100% of all seed dispersal events, suggesting that it is a keystone mutualist (Culver and Beattie 1978, Zelikova et al. 2008, Ness et al. 2009). Thus, if *P. chinensis* displaces *A. rudis* and fails to disperse seeds, it has the potential to reduce seed dispersal in invaded areas, leaving seeds more susceptible to predation by rodents as well as competition with parent plants. Here, we test the hypothesis that *P. chinensis* disrupts ant-seed dispersal mutualisms in a forest ecosystem in the southeastern United States. Specifically, we ask whether the presence of *P. chinensis* is associated with (1) changes in the structure of the native ant community and reductions in the abundance of the keystone mutualist *A. rudis* (2) disruption of seed dispersal mutualisms, and (3) reductions in the abundances of myrmecochorous plants.

## Material and methods

### *Natural history*

The native range of *P. chinensis* includes much of East Asia (Yashiro et al. 2010). Though the means and timing of its introduction into the US are unknown,

this species likely invaded the southeastern US from Japan some time before 1932 (Smith 1934) where it remained relatively inconspicuous with small colonies of only a few hundred workers for several decades (MacGown 2009). However, in the past ten years *P. chinensis* has become widespread and is now locally abundant in parts of Alabama, Georgia, North Carolina, South Carolina, Tennessee and Virginia, with viable colonies as far north as New York state (Guénard and Dunn 2010).

We conducted this study from May to July of 2009 at the 232-ha Historic Yates Mill County Park, a mature closed-canopy, mesic deciduous forest in Raleigh, North Carolina, USA (35° 43' N and 78° 41' W). Temperature in the area ranges from a minimum of -1 °C in January to a maximum of 32 °C in July with mean annual precipitation of 1052 mm yr<sup>-1</sup>. Historic Yates Mill County Park is a conservation area and is dominated by *Pinus taeda*, *Quercus spp.*, *Carya spp.* and *Acer rubrum*. It is adjacent to agricultural land. The understory consists of deciduous seedlings and numerous myrmecochorous plant species (*Asarum canadense* L., *Hexastylis arifolia* (Michx.), *Trillium spp.*, *Viola rotundifolia* (Michx.), *Sanguinaria canadensis* L. Our study focuses on two related myrmecochorous plant species in the family Aristolochiaceae (Birthwort), *A. canadense* and *H. arifolia*. We used seed *A. canadense* for all seed removal experiments, which has similar size and weight seeds to those of *H. arifolia* (Canner 2010). Elaiosome-bearing seeds remain attractive to ants for a year (Hughes and Westoby 1990).

We haphazardly selected 29 invaded plots where *P. chinensis* was present and paired these with 29 intact plots (where *P. chinensis* was absent). Each plot was 10 m × 10 m. Invaded plots were in areas in which we observed *P. chinensis* foragers or active colonies. The intact plots were chosen by walking 20 m (twice the maximum distance of foraging by *P. chinensis* (Guénard pers. observation) in a haphazardly chosen direction from the invaded plot. The intact plots were established where no *P. chinensis* foragers or nests were observed. Once the plot was selected, we extensively searched for *P. chinensis* workers and nests. This paired design has the advantage of controlling for environmental factors that might covary with the effects of *P. chinensis*.

### ***Effect of P. chinensis on native ant assemblages***

To sample the ants in each plot, we placed three pitfall traps, arranged in a triangle, with sides of 5 m. Pitfall traps were specimen cups 55 mm in diameter and 75 mm deep. These were partially filled with soapy water, buried flush with the ground, and left open for 24 hours during non-rainy weather. Ants were sampled once at each plot. Pitfall traps are an effective method to sample the subset of ant species that are active ground foragers, which includes both *P. chinensis* and the native *A. rudis* (Bestelmeyer et al. 2000).

### ***Effect of P. chinensis on seed dispersal***

We assessed the impact of *P. chinensis* on seed dispersal rates of bloodroot (*A. canadense*), a common myrmecochorous species in Yates Mill County Park. The species is a widespread, shade-tolerant perennial that occurs in forest understories throughout the eastern US (Damman and Cain 1998). At each plot, we placed three seed depots of 10 seeds each at the corners of the triangles described above (prior to the placement of pitfall traps). Seeds were placed on wooden cards in the invaded plots and on laminated index cards in the intact plots. Wooden cards were used in the invaded plots because *P. chinensis* workers appeared to have some difficulty walking on the laminated index cards, a difficulty not shared by any of the other species. The wooden cards and index cards were similar in size and thickness. A pilot experiment demonstrated that card type (wooden vs. laminated paper) did not influence seed removal rates by native ant species. At each bait station, we recorded the identity of the ant species removing the seeds as well as the time taken to discover and remove the seeds from each of the cards for 1 hour or until all of the seeds were removed, whichever came first. Seed presentations were conducted between the hours of 0900 and 1500 to coincide with a period of active foraging for most species in the study region (Fellers 1989).

### ***Habitat characteristics***

Within each plot we measured a suite of habitat variables representing the

physical structure of the habitat within a 1-m radius circular plots centered on each card ( $n = 3$  per plot) to determine what characteristics, other than the presence of *P. chinensis*, might differ between invaded and intact plots. These included number of logs ( $> 5$  inches in diameter), number of branches (1-5 inches in diameter) and number of sticks ( $< 1$  inch in diameter).

### ***Comparison of the effect of *P. chinensis* with the invasive Argentine ant***

We calculated the effect sizes of *P. chinensis* on the number of *A. rudis* workers and on the number of seeds removed as the log-response ratio of the mean of the response variable in the presence of *P. chinensis* species divided by the mean of the response in the absence of the invasive species (following Rodriguez-Cabal et al. 2009). A negative effect size indicates that the invasive species reduced the number of workers present and seeds removed. We performed a one-sample t-test to compare the magnitude of the impact of *P. chinensis* with the impact of the Argentine ant as determined in a previous study (Rodriguez-Cabal et al. 2009).

### ***Data analysis***

We performed paired t-tests to compare several characteristics of invaded and intact plots: total number of seeds removed; number of seeds removed by each ant species; time to removal of the first seed; number of myrmecochorous plants;

and number of logs, branches and sticks. We log transformed time to removal of the first seed to improve normality and reduce heteroscedasticity. Finally, we performed separate linear regression analyses to examine the relationship between abundances of *P. chinensis*, *A. rudis* and myrmecochorous plants against the habitat variables representing the physical structure of the habitat in invaded and intact plots.

## Results and discussion

Plants that depend on ants as seed dispersers often rely disproportionately on a single ant species or species group (Gove et al. 2007, Ness et al. 2009), making them especially vulnerable if the behaviour or abundance of the keystone mutualist is altered (Giladi 2006). Many plant species in the eastern US rely on *A. rudis* for seed dispersal (Ness et al. 2009). If the abundance of this ant species group is decreased by the invasion of *P. chinensis*, seed dispersal hence has the potential to be altered. In addition to the invasive ant *P. chinensis* we also found *A. rudis*, *Amblyopone pallipes*, *Formica subsericea*, *Camponotus pennsylvanicus*, *C. castaneus* and *C. americanus* within invaded plots. In the intact plots we found *A. rudis*, *F. subsericea*, *C. pennsylvanicus*, *C. castaneus*, *C. americanus* and *Temnothorax curvispinosus*. However, species density was greater in invaded plots (mean  $\pm$  SE,  $2.13 \pm 1.06$ ) than intact plots ( $1.43 \pm 1.04$ ) ( $t = 2.25$ ,  $n = 23$ ,  $P < 0.05$ ). We found that the number of *A. rudis* workers was 96% lower in invaded than in intact plots ( $t = -4.58$ ,  $n = 23$ ,  $P < 0.0001$ ; Fig VI-3).

Additionally, we found *A. pallipes* only in invaded plots ( $t = 2.75$ ,  $n = 23$ ,  $P < 0.05$ ) and only three workers of *T. curvispinosus* in intact plots. Conversely, the presence of *P. chinensis* was not associated with the number of individuals of *Formica subsericea* ( $t = 0.65$ ,  $n = 23$ ,  $P = 0.52$ ), *C. pennsylvanicus* ( $t = 0.78$ ,  $n = 23$ ,  $P = 0.44$ ), *C. castaneus* ( $t = 1.04$ ,  $n = 23$ ,  $P = 0.31$ ) or *C. americanus* (we found only two workers of *C. americanus*, one at an intact plot and one at one invaded plot). These results are similar to results from Guénard and Dunn (2010), who reported that species of both *Formica* and *Camponotus* were either more common where *P. chinensis* was present or unaffected by the presence of *P. chinensis*. Studies on other, more well-studied, invasive species have found that not all native ant species are equally affected by the spread of an invasive species (Porter and Savignano 1990, Suarez et al. 1998, Holway et al. 2002, Lessard et al. 2009). One possible explanation for the dramatic drop in *A. rudis* abundance could be that *P. chinensis* is preferentially preying upon *A. rudis*. *Pachycondyla chinensis* has been found to kill *A. rudis* workers in direct interactions in laboratory experiments (Bednar 2010). Another possible explanation for this pattern may be that *P. chinensis* and *A. rudis* compete for nest sites. As is the case with many ant invasions, distinguishing between the effects of interspecific competition and predation is often challenging (Holway et al. 2002).

The efficiency of a seed disperser is the contribution of a disperser to the fitness of a plant, and this measure involves both the quantity and quality of dispersal (Schupp 1993). The quantitative component is the number of seeds

dispersed and the quality depends on the probability that a dispersed seed will become an adult. We found that the number of seeds removed per plot was 70% lower in invaded than in intact plots ( $t = -10.69$ ,  $n = 29$ ,  $P < 0.0001$ ). In invaded plots, the majority of seeds were removed by *P. chinensis*, which accounted for 97% of the 243 seeds removed, whereas *A. rudis* was responsible for 96% of the 773 seeds removed in the intact plots (Fig VI-4). Consequently, *P. chinensis* affects seed removal and potentially dispersal by removing fewer seeds than does *A. rudis* in intact areas. A growing body of work shows that invasive ants seem to be inferior seed dispersers to native ants, often finding seeds more slowly (Gómez and Oliveras 2003). In our system, because of the numerical dominance of *P. chinensis* in invaded plots and their relatively low rates of seed dispersal, seeds in invaded plots were discovered two times more slowly than they were in intact plots ( $16.87 \pm 1.67$  minutes vs.  $8.36 \pm 1.31$  minutes) ( $t = 4.01$ ,  $P < 0.0003$ ).

As a consequence of the low quantity of seed removed by the invasive *P. chinensis*, many seeds in invaded plots may simply not be dispersed. As for those seeds that are removed by *P. chinensis*, their fate is unknown. Eguchi (2004) suggested that *P. chinensis* in its native range might act as a granivorous species. Another study considered *P. chinensis* a poor seed disperser despite being native to a region where elaiosome-bearing seeds are common (Yashiro et al. 2010). This invasive ant has been described as a termite specialist but also consumes other animals in its invaded range (Guénard and Dunn 2010). Seeds dispersed by *A. rudis* are generally left in middens inside nests (which are either

in logs or the litter) or carried out of nests into the leaf-litter (Culver and Beattie 1980). We do not know if seed removed by *P. chinensis* are being predated or dispersed. However, because *P. chinensis* nests tend to be inside logs, we presume that most of the seeds collected by *P. chinensis* end up buried in or beneath logs, which likely affects the quality of the seed dispersal. We do not know whether seeds deposited under logs have higher (as would be the case if logs serve as 'nurse logs') or lower germination success than those on the soil surface or on the trash pile.

*Hexastylis arifolia* was the only myrmecochorus plant species conspicuous at the time our study was conducted because the leaves and flowers of *A. canadense* die after the growing season, leaving only the rhizome to overwinter (Cain and Damman 1997). The density of *H. arifolia* was 50% lower in invaded plots ( $1.43 \pm 0.30$ ) than in intact plots ( $3.14 \pm 0.65$ ) ( $t = -2.42$ ,  $n = 29$ ,  $P < 0.05$ ). This result is reconcilable with the effects of reduced levels of seed dispersal caused by the dramatic reduction of *A. rudis* (Ness et al. 2009, Zelikova et al. 2008). Moreover, *H. arifolia* seeds do not persist in the seed bank (Giladi 2004). Consequently, *A. rudis* is clearly an important seed disperser - the richness of myrmecochorous plants in temperate hardwood forests of eastern North America is often positively related to the abundance of *A. rudis* (Mitchell et al. 2002), and Zelikova et al. (2008) found that *A. rudis* was responsible for ~99% of seed dispersal events in Great Smoky Mountains in the southeastern US. Other studies of the effects of invasive ants on seed dispersal mutualisms have found similar results. For example, the effect of *L. humile* on the plant community

composition of the Fynbos in South Africa arises because of the disruption of seed dispersal mutualisms (Bond and Slingsby 1984, Christian 2001). However, plants in the Fynbos do not rely on a single species of ant (Christian 2001). In our system (and perhaps more generally in forests of the eastern US), a single ant species complex (*A. rudis* is probably a complex of 3-4 species) is responsible for the majority of seed dispersal events. Although *P. chinensis* does not appear to cause declines in the abundance of all ant species (Guénard and Dunn 2010), it appears to affect the seed disperser and in doing so affects the process, seed-dispersal, that species mediates.

The differences in the densities of *H. arifolia* between invaded and intact plots could have resulted from factors other than changes in seed dispersal. For example, it may have arisen because of differences in rates of herbivory in intact and invaded plots, if *P. chinensis* does not prey on the herbivores of *H. arifolia* to the same extent as native ant species do (Holway et al. 2002, Styrsky and Eubanks 2010). However, the percentage of *H. arifolia* with apparent damage by herbivores did not differ between invaded ( $12 \% \pm 3.60$ ) and intact plots ( $7 \% \pm 2.60$ ) ( $t = 1.08$ ,  $n = 23$ ,  $P = 0.29$ ). Additionally, we estimated possible rates of predation on invertebrates in intact and invaded plots by placing four wax-worms (previously frozen) at the center of each plot and recorded the number of worms removed after 24 hours. We found no difference in the number of wax-worms removed in the invaded ( $3.9 \pm 0.1$ ) and intact ( $4.0 \pm 0$ ) plots ( $t = -1.00$ ,  $n = 10$ ,  $P = 0.34$ ). Together, these results suggest that the indirect positive effects of deterring herbivores insects by *P. chinensis* on *H. arifolia*, if there are any, do not

differ from the effects of native ant species. Consequently, the lower density of *H. artifolia* in invaded plots is likely due to the disruption of the ant-seed dispersal mutualisms.

An alternative explanation for the differences in *H. arifolia* abundance between intact and invaded plots is that the plots differed in their abiotic or biotic conditions. Abiotic and biotic variables might influence the establishment of myrmecochorous plants in this system, and that these same abiotic and biotic variables also influence the abundances of *A. rudis* and *P. chinensis*. We found more logs in plots invaded by *P. chinensis* than in intact plots (invaded =  $0.88 \pm 0.11$  vs. intact =  $0.43 \pm 0.10$ ;  $t = 3.14$ ,  $n = 29$ ,  $P < 0.05$ ), but we found no differences in the number of branches ( $t = -1.24$ ,  $n = 29$ ,  $P = 0.22$ ) and sticks between invaded and intact plots ( $t = -0.65$ ,  $P = 0.51$ ). From a pitfall survey conducted at each plot we did not find a relationship between the number of logs and *P. chinensis* abundance ( $R^2 = 0.05$ ,  $P = 0.27$ ), nor was there a relationship between the abundance of *A. rudis* and the number of logs ( $R^2 = 0.009$ ,  $P = 0.62$ ). Likewise, there was no relationship between the number of logs and the density of myrmecochorous plants in invaded s ( $R^2 = 0.07$ ,  $P = 0.12$ ) or in intact plots ( $R^2 = 0.08$ ,  $P = 0.16$ ). These results suggest the absences of abiotic effects on the presence of *P. chinensis*, and on the number of myrmecochorous plants in invaded plots.

We used meta-analysis to compare the effects observed in this study to the effects of Argentine ants, *Linepithema humile*, on seed dispersal mutualisms. We found the effects of *P. chinensis* and *L. humile* to be quantitatively similar: the

presence of the invasive Argentine ant led to a 92% reduction in the abundance of native ant seed dispersers (Rodriguez-Cabal et al. 2009), and the presence of *P. chinensis* led to a the 96% reduction ( $t = -0.34$ ,  $n = 7$ ,  $P = 0.74$ ). Additionally, the effect of *P. chinensis* on the number of seeds dispersed did not differ from the effects of Argentine ants ( $t = 0.81$ ,  $n = 18$ ,  $P = 0.43$ ): plots invaded by *P. chinensis* had, on average, 70% fewer seeds dispersed, similar to the 76% reduction in the number of seeds dispersed in plots with Argentine ants (Rodriguez-Cabal et al. 2009). While there is some question as to whether invasive ants such as *S. invicta* and *L. humile* become established in plots where native ant diversity is already reduced or whether they reduce diversity (Sanders and Suarez 2010, Stuble et al. 2011), several lines of evidence strongly suggest that *P. chinensis* is responsible for the declines in the abundance of the keystone seed-dispersers ant in this system. First, our study plots occur in protected forests that have been minimally impacted by human disturbance over at least the past several decades. Other invasive ants (*S. invicta*, *L. humile*), which are sometimes associated with disturbance, are common near our study plots but have not been detected to date in our study plots. Second, our matched pair design should effectively account for much of the variation in environmental or habitat characteristics, other than the presence of *P. chinensis*.

In conclusion, our results indicate that *P. chinensis* is associated with the disruption of an ant-plant seed dispersal mutualism, and is potentially reducing abundances of ant-dispersed plants. Our study is in line with previous studies that have documented the negative effects of invasive ants on ant-plant seed

dispersal mutualisms (Bond and Slingsby 1984, Christian 2001, Carney et al. 2003, Ness and Bronstein 2004, Rodriguez-Cabal et al. 2009), and documents this detrimental effect of an understudied invasive ant species on an important ecological interaction. Finally, our study focused on two myrmecochorous species. Examining the community-level impacts of invasive species, or the impacts on the suite of myrmecochorous species, would be an exciting and largely untapped area for future research.

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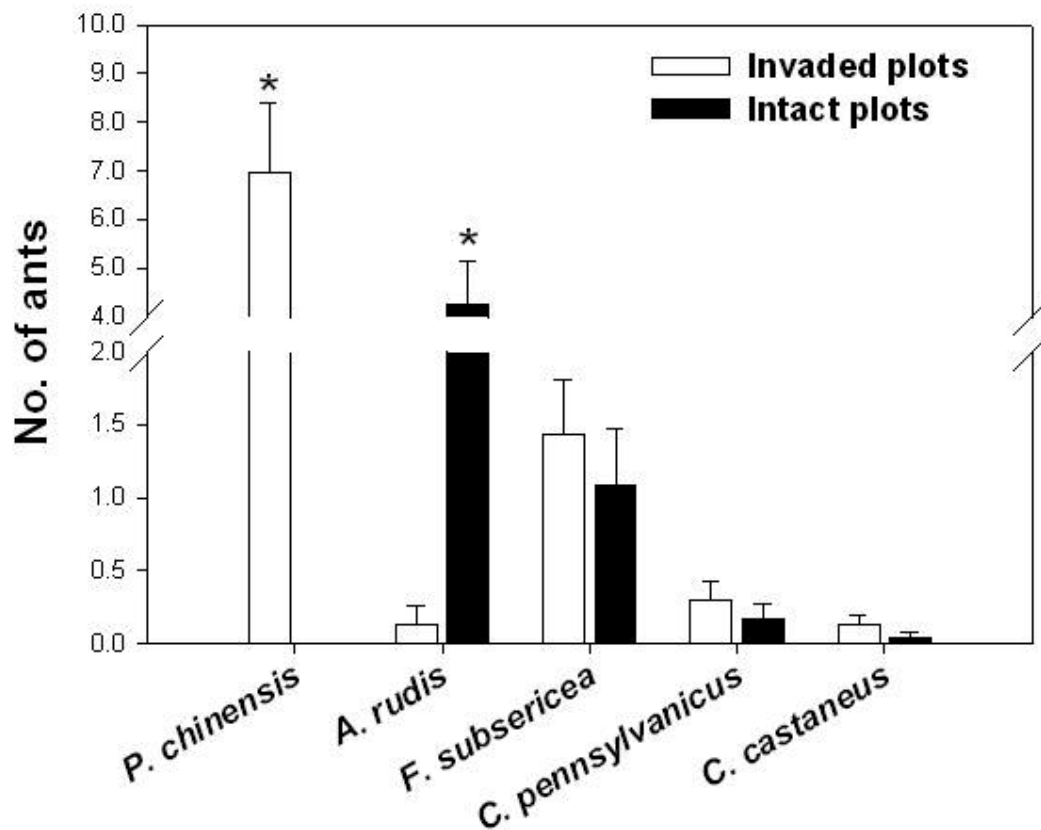


**Figure VI-3.** Comparison of the number of ants (mean  $\pm$  1 S.E.) in plots invaded by *P. chinensis* invaded and intact plots. Pitfall traps lacking *P. chinensis* were recorded as intact sites ( $n = 29$ ). Significant differences in number of ants between invaded and intact sites are noted with an asterisk (*P. chinensis*  $t = 4.52$ ,  $P < 0.0002$ ; *A. rudis*  $t = -4.58$ ,  $P < 0.0001$ ; *F. subsericea*  $t = 0.64$ ,  $P = 0.52$ ; *C. pennsylvanicus*  $t = 0.78$ ,  $P = 0.44$ ; *C. castaneus*  $t = 1.03$ ,  $P = 0.31$ ).

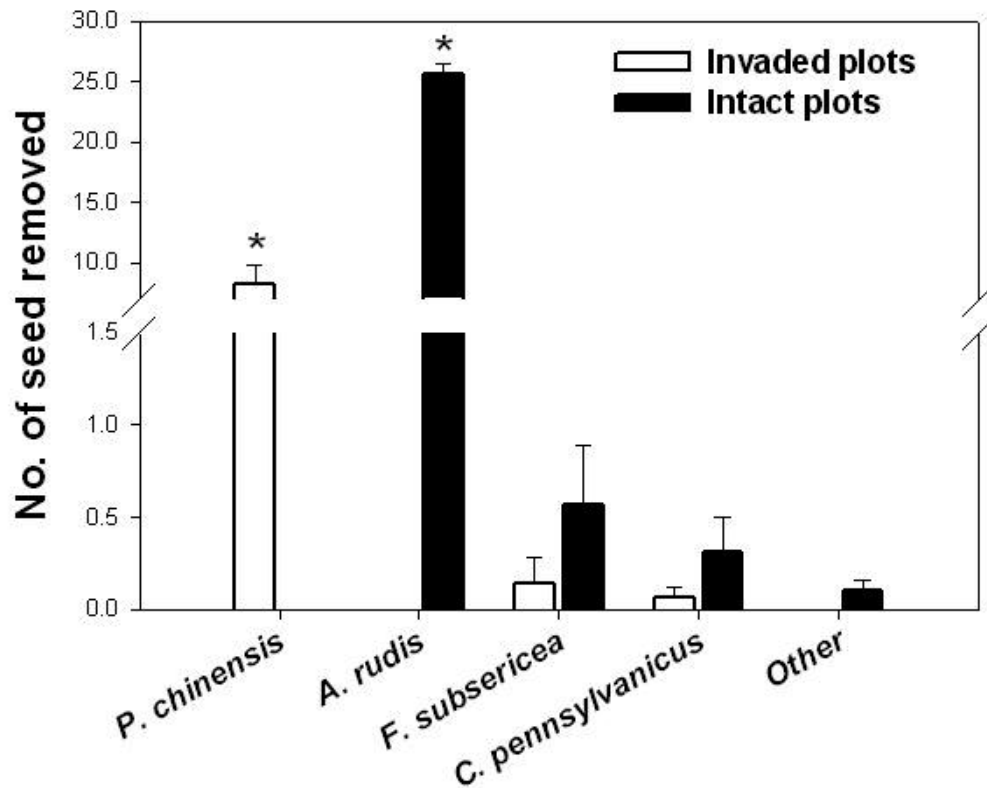


**Figure VI-4.** Mean ( $\pm 1$  S.E) number of *A. canadense* seeds removed by ants species in 29 invaded and intact plots. Significant differences in number of seeds removed by each ant species between invaded and intact sites are noted with an asterisk (*P. chinensis*  $t = 5.24$ ,  $P < 0.0001$ ; *A. rudis*  $t = -28.89$ ,  $P < 0.0001$ ; *F. subsericea*  $t = -1.27$ ,  $P = 0.21$ ; *C. pennsylvanicus*  $t = -1.21$ ,  $P = 0.23$ ; others (ants and insects)  $t = -1.80$ ,  $P = 0.08$ ).

## **CHAPTER VII COEXTINCTION OF KEYSTONE MUTUALISTS LEADS TO DISASSEMBLY OF INTERACTION WEBS**

The Following section is a slightly modified version of a paper in preparation:

Rodriguez-Cabal, M.A., Barrios-Garcia, M.N, Amico, G.C., Aizen, M.A. and N.J. Sanders. *In prep.* Coextinction of keystone mutualists leads to disassembly of interaction webs.

The use of “we” in this chapter refers to my co-authors and me. As the lead author of this article I was responsible for this paper. M.A.R.C. and N.J.S. designed research, M.A.R.C., B.G.M.N. and G.C.A. performed research, M.A.R.C. analyzed data and M.A.R.C., B.G.M.N., G.C.A., M.A.A. and N.J.S. wrote the paper.

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Abstract

The loss of the keystone species may have disproportionate effects on the rest of the community, especially if keystone species are embedded in co-evolved interaction webs. Yet, the non-trophic effects of species declines and extinction on interaction webs are poorly understood, because it is challenging to study indirect effects in complex interaction webs and because perturbations to the interaction web can be attenuated by functional redundancy. We took advantage of ongoing invasions by exotic herbivores (ungulates) and frugivores (German wasps) in Patagonia, Argentina to examine the mechanisms and consequences of the disassembly of co-evolved interaction webs. We found that the loss of the host of the keystone mistletoe *Tristerix corymbosus*, leads to the disassembly of the mutualistic interaction web. When the host is directly affected by exotic herbivores and an exotic frugivore, there are indirect effects that lead to local extinction, through the loss of the mistletoe, two key seed dispersers (the marsupial *Dromiciops gliroides* and the bird *Elaenia albiceps*), and a pollinator (the hummingbird *Sephanoides sephaniodes*). Taken together, our results demonstrate that the gains and losses of species are both consequences and drivers of global change that lead to cascading co-extinctions, and illuminate the different ways in which interaction webs can be disassembled.

Introduction

Interactions, both direct and indirect, are the ties that bind species together in ecological communities (Holt 1977, Wootton 1994, Strauss 1991). And while much remains to be learned, it is clear that interactions involving key species (i.e., keystone species) play essential roles in connecting numerous other species to one another in interaction webs (Paine 1966, Estes et al. 1998). Moreover, particular types of interactions in which those keystone species are involved can be especially important for the maintenance of community stability (Estes et al. 1998, Tylianakis et al. 2008, Aizen et al 2012). More generally, there is growing empirical and theoretical support for the hypothesis that connectance (i.e., the observed number of interactions relative to the maximum) promotes stability in mutualistic interaction webs (Okuyama and Holland 2008). However, not all the interactions are equal; the keystone mutualist hypothesis posits that interactions with particular mutualists prevent a cascade of linked extinctions such that the loss of a keystone mutualist would lead to community disassembly (Gilbert 1980). The idea that connectance promotes stability and that the loss of keystone mutualisms leads to disassembly relies on the notion that mutualisms and the species engaged in them are fundamental to maintaining the structure and diversity of ecological communities (Koh et al 2004, Kaiser-Bunbury et al. 2010, Okuyama and Holland 2008, Aizen et al. 2012).

In this study, we take advantage of an ongoing natural experiment triggered by the invasion by a suite of exotic species to examine whether

disruption of mutualisms and the loss of keystone mutualists leads to the disassembly of a highly co-evolved interaction web in Patagonia, Argentina (Fig VII-5). The pivotal nodes of this interaction web consist of the southern-most hummingbird (*Sephanoides sephaniodes*), a hemi-parasitic mistletoe (*Tristerix corymbosus*), the most common mistletoe host and understory shrub (*Aristotelia chilensis*, Amico et al. 2009), and a highly endemic marsupial (*Dromiciops gliroides*, Amico and Aizen 2000). The hummingbird pollinates nearly 20% of the endemic woody genera in Patagonian forests (Armesto et al. 1996, Aizen 2003). The mistletoe (*T. corymbosus*) is the primary food resource for the hummingbird during the winter (Aizen 2003). And the marsupial (*D. gliroides* - the only extant member of the marsupial order Microbiotheria), while presumed to be the only seed disperser of 16 fleshy-fruited species (Amico et al. 2009), is the only known disperser the mistletoe in Patagonia (Amico and Aizen 2000), and mistletoe fruit is an important food staple for the marsupial (Rodriguez-Cabal and Branch 2011). Furthermore, after passing through the gut of *D. gliroides*, most defecated seeds of the mistletoe stick to branches of *A. chilensis* (Amico and Aizen 2000). Finally, the fruits of *A. chilensis* are an important food resource for the White-crested Elaenia (*Elaenia albiceps*), the most common seed-dispersing bird in these forests that is involved in the dispersal of seeds from > 82 plant species (Amico and Aizen 2005). Moreover, the probability of germination for seeds of *A. chilensis* that are dispersed by *E. albiceps* is nearly 3× higher than for non-dispersed seeds (Valdivia and Simonetti 2007). Because these strong, and highly co-evolved interactions are in many instances obligate, any reduction in the

abundance or alteration of the behavior of any of these species has the potential to disassemble this interaction web and in turn dramatically reduce the highly endemic biodiversity of Patagonian forests.

Livestock (*Bos taurus*) were introduced to these forests by Europeans in the late eighteenth century (Veblen et al. 1992), and game animals such as red deer (*Cervus elaphus*) and fallow deer (*Dama dama*) were introduced in 1904 (Jacksic et al. 2002). All are widespread in these forests (occupying >50% of the forests; Jacksic 1998). These exotic ungulates are the main source of disturbance in the temperate forests of Patagonia (Veblen et al. 1992, Vazquez 2002, Vazquez and Simberloff 2003).

Material and methods

Study area and natural history

We conducted our research in Nahuel Huapi National Park (705,000 ha) and Arrayanes National Park (1,753), in northwestern Patagonia, Argentina. The native forest vegetation in the study area belongs to the Subantarctic biogeographical region, which is distinctive from the Neotropical forest of the rest of South America (Cabrera, 1976). This temperate forest is known for its high endemic flora and number of plant-animal mutualisms (Aizen and Ezcurra 1998). For example, more than 70% of the woody plants have vertebrate seed-dispersal mutualisms (Aizen and Ezcurra 1998).

We selected 26 sites for the study. Exotic ungulates are present at 13 of the sites, seven have only deer and six have cows and deer (invaded sites here after); while the other 13 sites have no exotic ungulates (intact sites). Sites were 25 x 25 m and were chosen haphazardly to incorporate the range of habitats found in each treatment. The most common trees, at all sites, are the evergreen southern beech (*Nothofagus dombeyi*), and the conifer (*Austrocedrus chilensis*). The understory is dominated by the shrub *A. chilensis* and a bamboo (*Chusquea culeou*). The two forest layers are well differentiated with tree canopy reaching up to 40 m height and understory reaching up to 5 m height.

Exotic ungulates

In the Austral summers of 2010 and 2011 we examined the direct effect of exotic ungulates on *A. chilensis* and their indirect effects on the interaction between the hummingbird, the mistletoe and the marsupial. We measured the following suite of biotic and physical variables in 25 m² circular plots haphazardly placed at each site and separate at least by 5 m (n = 4 per site): number of reproductive *A. chilensis* (>70 cm in height), number of reproductive mistletoes, number of seed dispersed and seedlings (those presenting the first two true leaves) of the mistletoe, and the complexity of habitat structure. As a measure of habitat complexity within each plot, we counted the number of contacts with a vertical pole (3 m height) for branches 5-10 cm in diameter and oriented < 45° relative to the ground and number of fruiting plants.

To quantify the effects of browsing by exotic ungulates on *A. chilensis* we conducted an exclosure experiment. In 2010 we planted twelve pairs of *A. chilensis* at three sites, each pair consisting of one *A. chilensis* fenced with 1.2-m high woven wire to prevent browsing by exotic ungulates, while the other *A. chilensis* was open to allow browsing (control). We counted the number of leaves in each *A. chilensis* at the beginning of the experiment and after 30 days. We determined the age of mistletoe hosts at three intact and three invaded sites. At each site, we extracted one increment core per host at c. 0.5 m above the ground from at least ten hosts. Due to the small diameter of the host trees/shrubs (0.5 to 150 cm dbh), all trees/shrubs cores we sampled included all the rings to the pith. Sampled individuals included the full range of host sizes present in the site. Trees/shrubs cores were mounted, sanded, and dated using standard dendroecological techniques (Stokes and Smiley 1968). We compared the frequency distribution of host ages between populations at intact and invaded sites performing a non-parametric statistic test of Kolmogorov-Smirnov.

In order to facilitate rapid surveys on the indirect effects of exotic ungulates on the presence-absence of the marsupial, the 26 study sites were grouped by presence or absence of mistletoe (see Rodriguez-Cabal and Branch 2011 for a detailed explanation). At sites with mistletoe, we concluded that marsupials were present if we found mistletoe seeds dispersed. If no dispersed seeds were found in the site, we used trapping to determine the presence of the marsupials. Trapping also was conducted in sites with no mistletoe. Within each site, we placed a 5 x 5 grid of Tomahawk-style traps about 5-m apart. Each trap

was placed between 1-2 m above ground in the shrub closest to the sample point. Traps were baited with apple and banana. Because the objective was to document presence, once a marsupial was trapped, we stopped trapping at the site. Sampling for presence-absence was continued for four nights if no the marsupial was captured (see Rodriguez-Cabal and Branch 2011 for a full explanations of trapping methods). We concluded that the marsupials were absent after four nights of trapping if no individual was captured.

Finally, during the austral winter of 2011, flowering season of the mistletoe (March-November, Aizen 2003), the number of hummingbird (visually and/or acoustically) was register using fixed-radius point counts (Ralph et al 1995) at eight sites. Because of the eruption of the volcano Puyehue-Cordon Caulle in the fall of 2011 we could not used the same set of sites, consequently we selected eight new sites. Additionally, because site with long history of disturbance by exotic ungulates do not hold mistletoe populations, we selected four sites in places were exotic ungulates were present but in very low densities. We pair these four sites with sites were exotic ungulate were absent (intact sites). At each site, point counts were conducted during the morning on days without rain and wind. The distance between points was always >300 m. Hummingbirds were counted at three 25 m fixed radius plots during a 10 min period (Vergara et al. 2010).

Exotic wasps

To evaluate the impact of German wasps on *A. chilensis*-seed dispersers mutualisms, we marked 20 immature fruits with small paper tags on each of 60 plants haphazardly chosen in three different treatments in the Arrayanes National Park. Twenty *A. chilensis* were marked in intact sites (poison treatment), 20 in invaded sites (non-poison treatments) and 20 in overabundance sites (protein + sugar treatment). The sites were separated at least 1 km, because German wasps travel 200 m on average from the nest during foraging (Sackmann et al. 2001). We reduced the abundance of German wasps using toxic baits (poison treatment) prepared with 0.1% Fipronil® mixed with 20 g of raw ground beef (Sackmann et al. 2008). This poison was developed to control only German wasps and does not affect the native fauna (Sackmann et al. 2008). The baits were placed in feeding stations made of 500 ml plastic bottles with both ends cut off. In order to increase the abundance of German wasps (protein + sugar treatment) we added baits containing 20 g of fish-scented cat food bait (Whiskas, Kal Kan Foods, Verno, CA) (D'Adamo et al. 2003), 20 g of raw ground beef and 20 g of honey. In the two treatments, feeding stations were hung between 1-2 m above ground in a shrub on a 25 x 25 m grid. Poison and protein + sugar treatments were carried out before the fruits were ripe and during the entire fruiting season. To determine the abundance of German wasps, we hung in each of the 60 *A. chilensis* a 20 x 20 cm sticky trap. At monthly intervals during the fruiting season, we count the number of German wasps in each sticky trap.

Sticky traps were replaced each month. As a result, German wasps activity was significantly lower in plots in which we applied poison treatments 1.95 ± 1.82 (Mean $\pm$ S.D. per 20 x 20 cm sticky trap) relative to sites where we experimentally increased wasp activity (11.65 ± 5.14 in protein + sugar baits treatment).

At weekly intervals, we record the status of each marked fruit according to one of the following categories: developing fruit, ripe fruit, removed fruit, senescent fruit and predated fruit. Predated fruits are those where the pulp have been consumed without detaching the fruit/seed from the peduncle. We predicted that the German wasp, by preying upon fruits and being aggressive towards native birds, would reduce the number of fruits removed by seed dispersers. To test the impact of German wasps on frugivorous birds we conducted a bi-weekly bird census at intact, invaded and protein + sugar addition sites.

Overall direct and indirect effect of exotic species

We compile the results of each experiment and observational study conducted here and measured the direct and indirect effect of the exotic ungulates and the German wasp. We estimated the effect of these exotic species as the log-response ratio $[\ln(N_{PE}/N_{AE})]$ of the mean of the response variable in the presence of the exotic species (N_{PE}) divided by the mean of the response in the absence of the exotic species (N_{AE}) (Osenberg et al. 1999, Rodriguez-Cabal et al. 2009). The effect of exotic species is significant if the confidence intervals do not overlap zero.

Results and discussion

The presence of exotic ungulates has led to the disassembly of this highly co-evolved interaction web. *Aristotelia chilensis* is a preferred forage for both deer and cows (Veblen et al. 1992, Vazquez 2002), and as a result is directly affected by the presence of exotic ungulates: the density of *A. chilensis* is 16× greater in sites where these exotic species are absent (hereafter “intact sites” than in invaded sites (Fig VII-6a). We excluded deer for one month and found that 99% of *A. chilensis* leaves outside of the deer exclosures were removed by deer (Fig VII-6b). Mistletoe plants are common in these forests, and they appear to be specialists on *A. chilensis* (García et al. 2009): more than 85% of the plants parasitized by the mistletoe were *A. chilensis*. Indeed, the density of mistletoes was 83× greater in intact sites than in invaded sites (Fig VII-6c). Thus, by preferentially browsing on *A. chilensis*, exotic ungulates may indirectly affect the persistence of the keystone mistletoe, on which many other species rely.

The ungulates affect more than just *A. chilensis*. In fact, they affect the entire plant community (Veblen et al. 1992, Vazquez and Simberloff 2004). Total plant cover in the understory was 35× greater in intact sites than in invaded sites ($t_{25} = 19.51$, $P < 0.0001$). Consequently, habitat complexity was 20× lower in invaded sites than in intact sites ($t_{25} = 16.24$, $P < 0.0001$). Habitat characteristics such as the abundance and diversity of food resources, nest sites, and distance to shelter influence the distribution of vertebrate frugivores (Fedriani 2005, Rodriguez-Cabal and Branch 2011), and in turn fruit-bearing plants: the density

of fruiting plants was 3× lower in invaded sites than in intact sites (Fig VII-6d). These changes in habitat structure and food availability also affected the marsupial (Rodriguez-Cabal and Branch 2011). In fact, we never captured marsupials at any of the invaded sites, though they were present at each of the 13 intact sites. Because mistletoe seeds must pass through the gut of the marsupial and be deposited on branches of its host (*A. chilensis*), the local extinction of marsupials undoubtedly affects mistletoes recruitment (Rodriguez-Cabal et al. 2007). Indeed this is the case: we did not detect any marsupial-dispersed seeds (Mean $\pm$ S.D. per plot; intact sites 5.35 ± 7.18 ; $t_{25} = 4.46$, $P < 0.0001$) or mistletoe seedlings at invaded sites (Mean $\pm$ S.D. per plot; intact sites 2.12 ± 2.48 ; $t_{25} = 4.89$, $P < 0.0001$).

Exotic ungulates clearly had short-term effects on the host plants and on plant community composition in the understory. But they also appear to shape age structure of shrubs in these forests (Fig VII-7). Namely, age structure of the host plants of mistletoes at invaded sites ranged from 28 to 56 years. In contrast, at intact sites, in addition to saplings of host plants, the host plants of mistletoes ranged from 6 (minimum age detectable with this technique) to 42 years.

Because the density of mistletoes was 83× lower at sites with exotic ungulates than at sites without exotic ungulates and since the mistletoe is the primary food resource for the hummingbird, then the density of hummingbirds should also be lower in invaded sites than in intact sites. And in fact, the density of hummingbirds in the winter declined as mistletoe density declined (Fig VII-8),

suggesting that exotic ungulates affect hummingbird pollinators through their effects on host plants, and in turn the parasites of those host plants.

The effects of the exotic ungulates on this co-evolved interaction web are dramatic, but perhaps not surprising given the density and sheer biomass of the ungulates ($3,015 \text{ kg km}^{-2}$, Flueck 2010) in this system. However, another exotic species in these Patagonian forests may have more subtle but equally disrupting effects on mutualistic interactions. The German wasp, *Vespula germanica*, arrived in the early 1980s in Patagonia (Farji-Brener and Corley 1998), and it has rapidly spread, becoming one of the most outstanding insect invasions ever recorded for the region (Farji-Brener and Corley 1998, D'Adamo et al. 2002) as it has done elsewhere (Tribe and Richardson 1994). One of the crucial features for the German wasp's success is its highly efficient foraging behavior, with workers frequently returning to non-depleted food sources (Farji-Brener and Corley 1998, D'Adamo et al. 2002). In these forests, the wasp predares fruits of *A. chilensis*. We found that the number of *A. chilensis* fruits that were removed by seed-dispersing birds was 3× lower in sites invaded by *V. germanica* and 6× lower in sites in which we temporarily increased activity of *V. germanica* (by stocking sites with protein + sugar baits) relative to sites where *V. germanica* was absent (where we applied poison treatments; $F_{2,57} = 75.94$, $P < 0.0001$). Across all sites, the number of seeds removed per *A. chilensis* shrub decreased significantly with increasing activity of German wasps (Fig VII-9). Moreover, the density of *E. albiceps*, the most important seed dispersing bird species, did not differ among sites prior to the onset of fruiting by *A. chilensis* ($F_{2,3} = 0.09$, $P = 0.916$). However,

the density of *E. albiceps* was 3× lower (Mean ± S.D. per site; intact sites 5 ± 2.83) at sites where we experimentally increased wasp activity and 1.5× lower (7.5 ± 3.54) in control plots than at the sites where we experimentally reduced (18 ± 2.82) wasp activity during the fruiting season ($F_{2,3} = 10.02$, $P = 0.047$).

Both direct and indirect interactions can lead to cascading co-extinctions and the disassembly of interaction webs (Koh et al. 2004, Brook et al. 2008, Dunn et al. 2009). Despite the obvious direct effects of exotic ungulates and the German wasp, using meta-analytic tools, we found that the indirect effects were greater than direct effects (Fig VII-10) on the stability of the interaction web. Specifically, browsing by exotic ungulates on *A. chilensis* reduced the number of available hosts for the keystone mistletoe, consequently indirectly affecting marsupial populations, which in turn reduced the number of fruiting plants dispersed by the marsupial and the *E. albiceps*. The only node of the interaction web that appeared to not be affected was hummingbirds. However, this may not reflect the long-term effect of exotic species on hummingbirds since the hummingbird relies on mistletoe during the austral winter. One possibility is that the home range of any one hummingbird is much larger than the area affected by our treatments or the effects of the exotic ungulates.

The effects of local extinctions on ecosystems are on par with other global change drivers (Hooper et al. 2012). Our results reveal that a suite of exotic vertebrate herbivores and exotic invertebrates lead to a cascade of linked extinctions resulting in the disassembly of a mutualistic plant-animal interaction web in Patagonia. Because of the importance of the hummingbird as a key

pollinator, and the marsupial and *E. albiceps* as key seed dispersers in Patagonian forests, we predict that the decline or loss of these vertebrates could lead to a dramatic decline in the highly endemic flora of these forests. However, these results are not limited to this special case in which an exotic species indirectly affects keystone interactions in Patagonia. Direct and indirect species interactions play an essential role in the maintenance of community structure in a variety of ecosystems (Holt 1977, Wootton 1994, Strauss 1991). Our study provides strong evidence of the importance of indirect interactions among disparate taxa that rarely, if ever, interact directly with one another. Moreover, our results highlight the importance of focusing on interactions among species to understand the causes and consequences of species loss from ecosystems.

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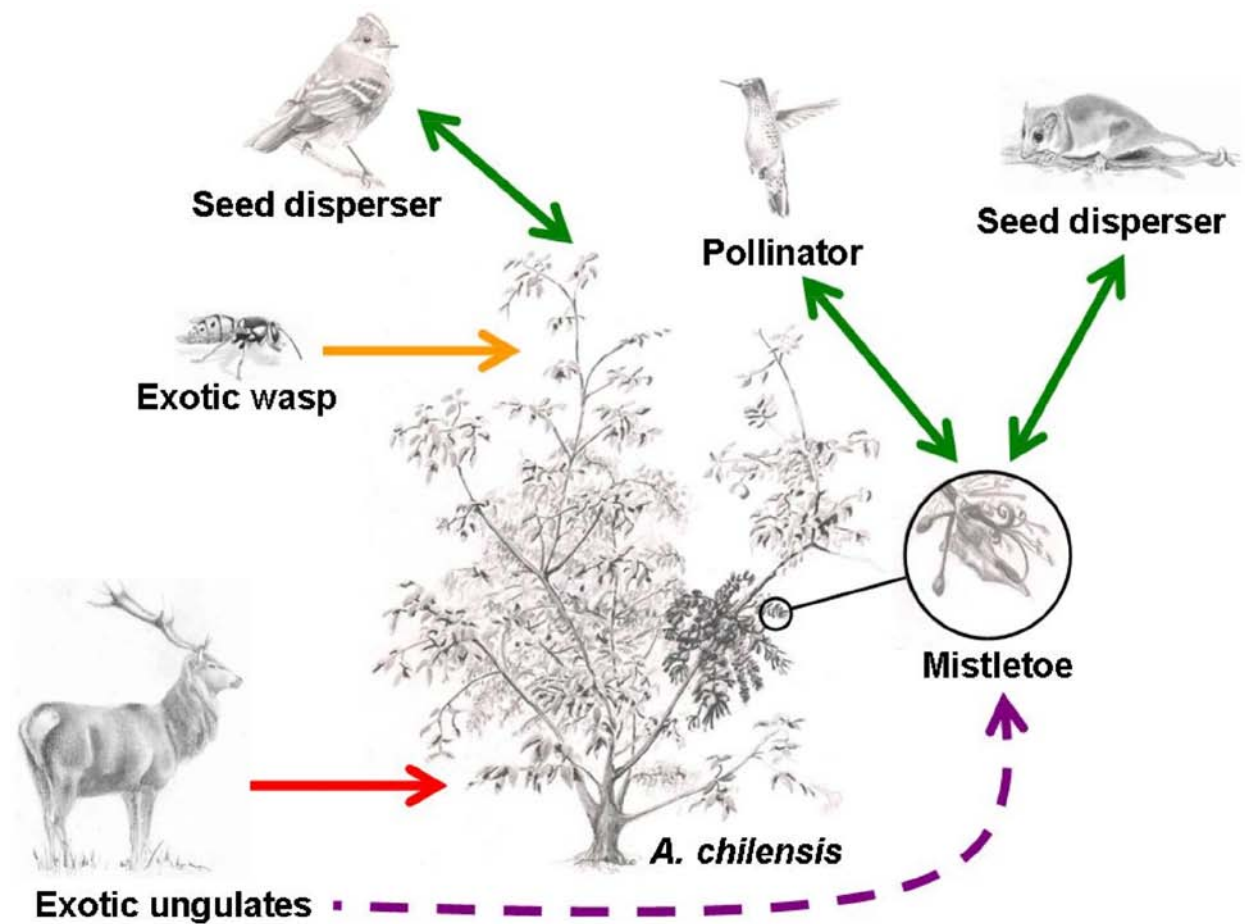
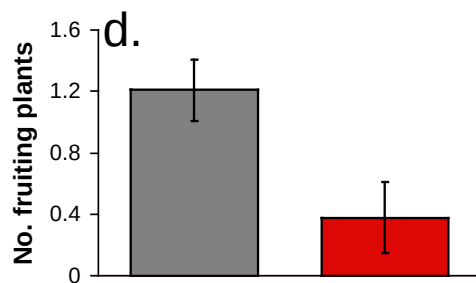
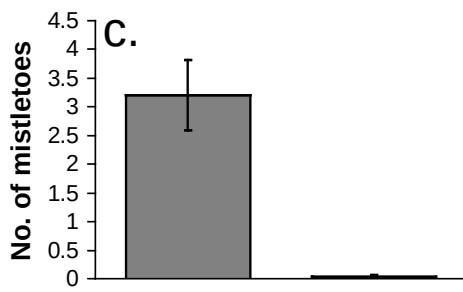
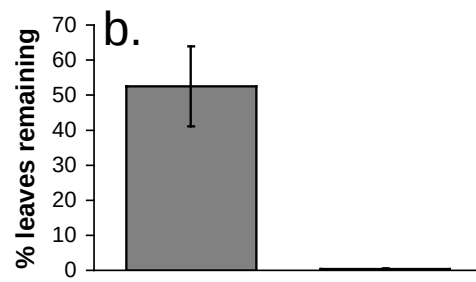
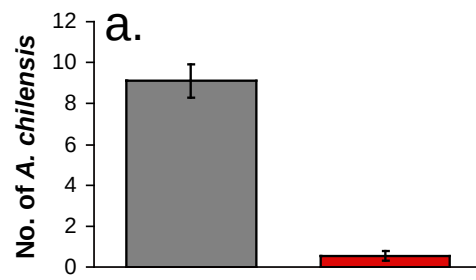


Figure VII-5. Interaction web showing the direct effects (solid arrows, yellow = fruit predation, red = herbivory, green = pollination and seed dispersal) of exotic species on *A. chilensis* and the indirect effect (dashed arrow, violet) on the keystone interaction between a hummingbird, a mistletoe, a marsupial and a bird. Exotic species are expected to negatively affect the population of *A. chilensis*, which in turn would have cascading effect on this unique triangle of native keystone mutualists (Drawings by Ezequiel Rodriguez-Cabal).

Figure VII-6. Direct effects of exotic ungulates. In the Austral summers of 2010 and 2011 we examined the direct effect of exotic ungulates at 13 sites with exotic ungulates (invaded sites) and 13 sites that have no exotic ungulates (intact sites) on the number of reproductive *A. chilensis* (>70 cm in height), number of reproductive mistletoe, and number of fruiting plants. In the summer of 2010 we quantified the effects of browsing by exotic ungulates on *A. chilensis* with an exclosure experiment. We found that: a. *A. chilensis* were 16× more abundant in intact (Mean ± S.D. per plot; intact sites 9.12 ± 3.72) than in invaded sites (0.55 ± 1.30 ; $t_{25} = 9.98$, $P < 0.0001$). b. Exotic ungulates consume almost 99% of the *A. chilensis* leaves outside the exclosure ($t_{23} = 4.58$, $P < 0.001$). c. Mistletoes was 83× more abundant in intact (Mean ± S.D. per plot; intact sites 3.21 ± 2.79) than in invaded sites (0.04 ± 0.19 ; $t_{25} = 8.18$, $P < 0.0001$). d. Fruiting plants were 3× less abundant at invaded than intact sites ($t_{25} = 4.08$, $P < 0.0001$).



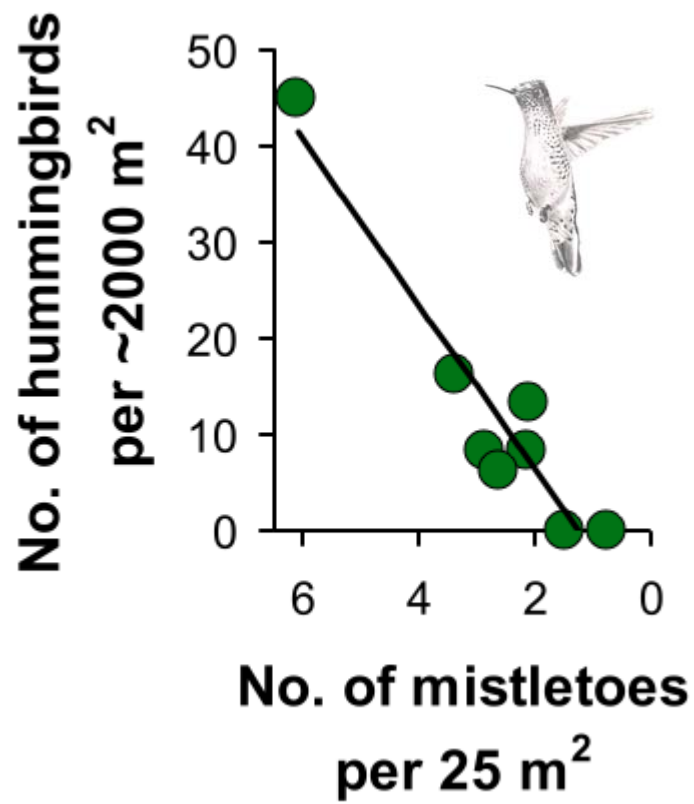


Figure VII-7. Hummingbird abundance during the austral winter decrease as the number of mistletoe plants decrease ($R^2 = 0.91$, $DF = 7$, $P < 0.001$).

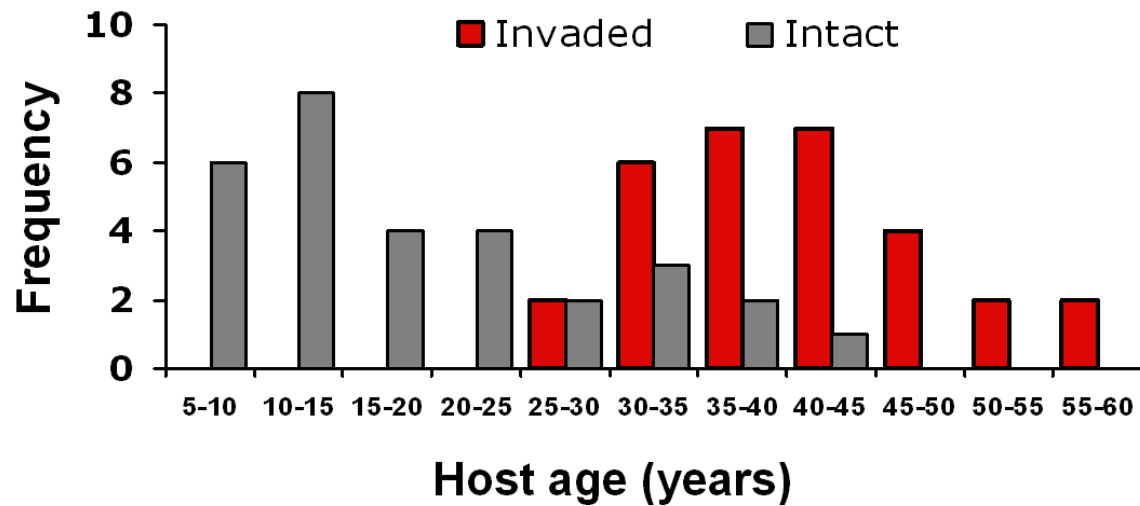


Figure VII-8. Using standard dendroecological techniques we determined the age structure of all possible mistletoe hosts at three intact and three invaded sites. Sampled individuals include the full range of host sizes present in the site. Estimated mistletoe host ages ranged between 6 and 42 years old in intact sites. In contrast, there were not infected host younger than 28 years at invaded sites (K-S = 0.383, $P < 0.0001$).

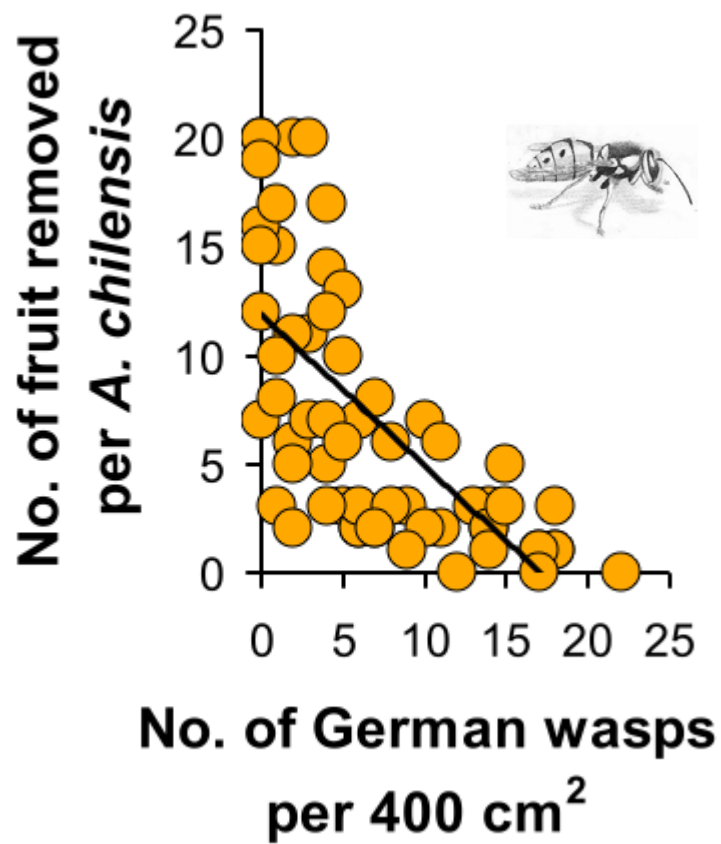


Figure VII-9. As German wasp abundance increase the number of seed removed decreased ($R^2 = 0.59$, $DF = 59$, $P < 0.0001$).

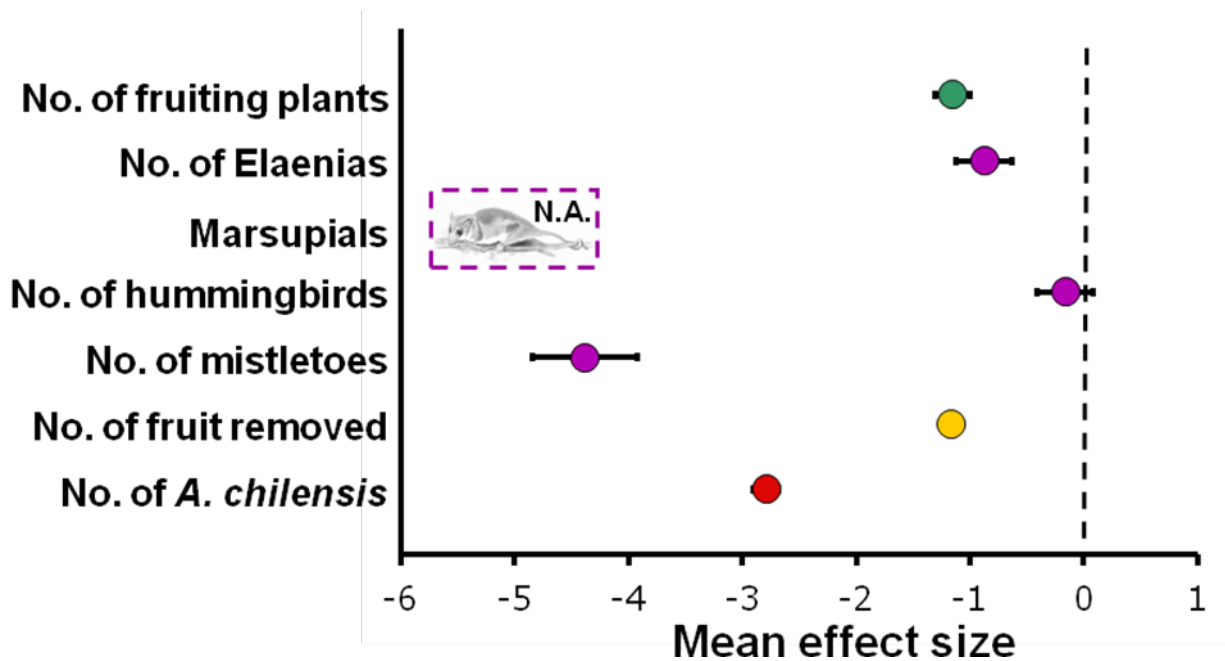


Figure VII-10. The effect size of exotic species [$\ln(N_{PE}/N_{AE})$] on the different response variables measured in this study. Error bars are 95% confidence intervals. The effect of exotic species is significant if the confidence intervals do not overlap zero (dash line). Violet indicates indirect effects, red depicts herbivory on *A. chilensis* by exotic ungulates, yellow shows the effect of German wasps on fruit removal and green shows number of fruiting plants dispersed by the marsupial and *Elaenia albiceps*. Because we used presence-absences to evaluate the indirect effects of exotic ungulates on the marsupial, we cannot calculate an effect size. However, we did not find marsupial at any of the invaded sites, but marsupial were presented in all the intact sites.

CHAPTER VIII. CONCLUSIONS

Conclusions

The rampant loss of biodiversity and the spread of invasive species are pervasive components of global change (Wardle et al. 2011, Simberloff et al. in press). An important research goal is to understand how the losses of native species and the gains of exotic species will impact terrestrial ecosystems. The losses of native species could be more dramatic if dominant species are lost and/or they play an essential role (i.e. keystone species). On the other hand, the impacts of exotic invasive species are greater when they add novel traits to the recipient ecosystem, become dominant in the community or when they disrupt species interactions. Despite that ecosystems worldwide are losing and gaining species, studies looking at the combined effects of species losses and gains in natural ecosystems are surprisingly rare. In Chapter II, I showed that positive interactions can counteract the effects of negative interactions, and in fact they do, and possibly modify the realized niche of a species, the realized niche of a species can never be larger than the fundamental niche. In Chapter III and IV, I found that the lack of information about failed species introductions and the tendency to report only species that have become invasive more than those that failed to invade result in an overestimation of the establishment success and invasion rates. In Chapters V, VI and VII I showed how species gains (exotic invasive species) lead to the disruption of plant-animal interactions due to the loss of native seed dispersers and/or native fruiting plants. Such losses compromised

the integrity of plant-seed disperser interactions and resulted in a cascade of local extinctions. Taken together, Chapters V, VI and VII are the first to show that simultaneous gains and losses of species are both consequences and drivers of global change that can lead to under-appreciated cascading co-extinctions. However, I believe that these results are not limited to the results of these special cases (exotic ants, wasps and ungulates) in which an exotic species directly and indirectly affect plant-animal interactions. In conclusion, my findings emphasize how long-term plans to conserve biodiversity must not only focus in maintaining the elements that form biodiversity but also on the interactions among these elements, such as interspecific interactions, trophic webs and ecological networks.

References

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VITA

Mariano Alberto Rodriguez Cabal was born in Buenos Aires, Argentina in 1976. His interest in biology began when he was very young. Nature has always exhibited a powerful attraction to him. He studied in a religious high school and obtained a degree in economics. When he finished his secondary studies, he moved to San Carlos de Bariloche in the foothills of the Andes, in western Argentina. The magnificent environment around this city, which is within a national park, led him unequivocally to pursue university studies in biology.

In 1997, he began studying Biology at Universidad Nacional del Comahue. In July 2003, he graduated as a “Licenciado en Ciencias Biológicas.” Under the guidance of Dr. Marcelo Aizen and Dr. Andrés Novaro, he conducted his undergraduate thesis research on the effects of habitat fragmentation on a dispersal mutualism in the temperate forest of southwestern Argentina. After two years of fieldwork, he completed and defended his thesis, obtaining the highest grade.

In 2004, he received a Fulbright Scholarship to study abroad. In the next year, he moved to Florida, USA, where he started his master’s studies at the University of Florida in the Department of Wildlife Ecology and Conservation. During those years worked under the supervision of Professor Lyn C. Branch. This work was recognized with three grants. Twice he earned the Outstanding

Academic Achievement Award at UF. In December 2007, he defended his master's thesis.

In 2008, he started the PhD program in Ecology and Evolutionary Biology at the University of Tennessee, Knoxville. During his PhD he worked under the supervision of Professor Nathan J. Sanders. This work was recognized with from the US National Science Foundation. He also earned the Exceptional Performance as a Graduate Student Award and the Science Alliance Award. The doctoral degree was awarded in November 2012. On completing his studies, he will return to his country to contribute to the welfare of his people and the conservation of Argentina's biodiversity through teaching and research.