

## Indirect interactions in terrestrial plant communities: emerging patterns and research gaps

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**Abstract.** Indirect interactions occur when the effect of one species on another is mediated by a third species. These interactions occur in most multi-species assemblages and are diverse in their mechanistic pathways. The interest in indirect interactions has increased exponentially over the past three decades, in recognition of their importance in determining plant community dynamics and promoting species coexistence. Here, we review the literature on indirect interactions among plants published since 1990, using a novel synthetic framework that accounts for and classifies intervening species and mechanisms within trophic networks. The objectives of this review are: (1) to identify the geographical regions and ecosystem types where indirect interactions have been examined; (2) to summarize the information on the number of trophic levels examined in studies of indirect interactions; (3) to test whether the frequency of indirect interactions varies across environmental gradients; and (4) to identify the experimental approaches most commonly used in studies of indirect interactions. Studies examining indirect interactions in plants have been conducted primarily in the Northern Hemisphere, with a focus on grasslands and forests. The majority of studies (67%) examined two trophic levels. Indirect facilitation and apparent competition are the interactions that have been most frequently examined, with the latter being reported more frequently in relatively productive environments. Other indirect interactions reported include associational resistance, exploitative competition or facilitation, shared defenses, and trophic cascades. Generally, field experiments tested indirect interactions based on single target species. While the majority of studies on indirect interactions dealt with basic ecology issues, several studies have dealt with such interactions in the context of biological invasions (18%) and rangeland management (12%). This review allowed us identifying a number of research needs, including the study of non-feeding interactions and that for more realistic complex designs, explicitly testing indirect interactions across different trophic levels, in geographical regions that have been under-examined to date, and in stressful ecosystems.

**Key words:** apparent competition; associational resistance; herbivory; indirect facilitation; multi-species interactions; systematic review; trait-mediated indirect effects.

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### INTRODUCTION

Net interactions between two species are the

outcome of both direct and indirect effects of each species on the other (Bruno et al. 2003, Lortie et al. 2004, Callaway 2007). While direct

positive and negative plant interactions have received considerable attention (Aarssen 1992, Silvertown 2004, Schenk 2006, Callaway 2007, Brooker et al. 2008), comparatively few studies have examined indirect interactions, possibly due to the challenges posed by the need to use sets of three or more species vs. those of testing pairwise interactions (Strauss 1991, Wootton 1994, Callaway 2007).

Indirect interactions occur when the strength or direction of interactions between two species changes in the presence of a third species (Strauss 1991, Wootton 1994, Callaway and Pennings 2000, Callaway 2007). For instance, plant-plant interactions are mediated by herbivores (e.g., Beguin et al. 2011, Vesterlund et al. 2012), pollinators (e.g., Moeller 2004), mycorrhizal fungi (e.g., Facelli et al. 2010), soil microbes (e.g., Johnson et al. 2003), or another plant species (e.g., Schöb et al. 2013). Trait-mediated indirect effects can also occur when interactions among plants change the traits of the interacting species thereby altering interactions with other species at different trophic levels (Abrams 1995, Werner and Peacor 2003, Ohgushi et al. 2013).

Indirect interactions occur virtually in all multi-species assemblages and can play an important role in the assembly and coexistence of species, and promote diversity in complex communities (Levine 1976, Miller 1994, Levine 1999) or in non-transitive interaction networks (Aarssen 1992, Brooker et al. 2008) by mitigating strong direct effects (Berlow 1999).

A number of important hypotheses are associated with indirect interactions. These include commonly studied feeding interactions, yet most indirect effects correspond to non-feeding interactions (Kéfi et al. 2012). Indirect interactions include apparent competition, indirect facilitation, exploitative competition and facilitation, associational resistance, trophic cascades and shared defenses (see Table 1 for definitions of common terms and references). Apparent competition is defined as an antagonistic interaction that occurs when the effects of one plant species on the other are manifested through a common consumer such as an herbivore (Chaneton et al. 2010, Recart et al. 2013). Indirect facilitation is defined as a positive interaction that occurs when the effects of one plant species on the other occur through a common competitor, as for example in

networks of competing plants (Callaway and Pennings 2000, Schöb et al. 2013). Plants can also mediate effects between consumers resulting in apparent competition when an herbivore negatively alters the resource offer to other herbivores via changes in the phenotype of the plant (Kaplan et al. 2011), or conversely in indirect facilitation when these changes result in positive effects on the other herbivores (Vesterlund et al. 2012). When plants represent resources (e.g., seeds) without changing their phenotype the interaction is termed exploitative competition or facilitation (*sensu* Wootton 1994) depending on its outcome for the consumer species (Beard et al. 2013). Hence, indirect feeding interactions have been documented through a number of different mechanisms.

Associational resistance is defined as a positive interaction in which the influence of one plant on the other decreases the likelihood of the beneficiary species being detected by a consumer (Barbosa et al. 2009). This occurs when palatable beneficiaries are associated closely with unpalatable species (Callaway et al. 2005, Graff et al. 2013). Shared defense occurs in a similar interaction context, but the nearby unpalatable species presents adaptations to repel herbivores such as spines (Vandenberghe et al. 2009). Trophic cascades are strong interactions within food webs (Polis et al. 2000) and involve more than two trophic levels such as predators, herbivores and plants (Polis et al. 2000, Schmitz et al. 2000). These indirect interactions occur when plants change their resource offer (e.g., chemical composition) to herbivores that in turn affect their predators (Laws and Joern 2013). They can take place at the species or population level when a subset of the community is involved in the interaction, but also at the community level when they alter substantially the distribution of organisms or biomass of the entire system (Polis et al. 2000). Trophic cascades can also be conceptualized as top-down or bottom-up, when regulation within the interaction is exerted by an upper-level predator or the primary producers, respectively (Pace et al. 1999).

Two general frameworks have been proposed to conceptualize indirect interactions in ecology. Wootton (1994) proposed a framework to categorize these interactions using five hypotheses or mechanistic pathways: (1) interspecific competi-

Table 1. Main hypotheses tested regarding indirect interactions in terrestrial plants along with a concise definition and examples of reference articles.

Hypotheses tested	N (%)	Definition	Reference article(s)
Apparent competition	89 (41.6)	Antagonistic interactions occurring when the negative effects of one plant species on the other occur through a common consumer, such as an herbivore. Plants can also mediate these interactions through changes in their resource offer.	Burger and Louda (1994); Recart et al. (2013)
Indirect facilitation	76 (35.5)	Positive interactions occurring when the positive effects of one plant species on the other occur through a common competitor. Plants can also mediate these interactions through changes in their resource offer.	Callaway and Pennings (2000); Schöb et al. (2013)
Exploitative competition and facilitation	20 (9.3)	Negative or positive interactions occurring when two species interact through resource consumption where the resource is a plant species.	Samson et al. (1992); Vesterlund et al. (2012)
Associational resistance	19 (8.9)	Positive interactions occurring when a palatable beneficiary is spatially clustered with nearby unpalatable species making it undetectable for herbivores.	Mulder and Ruess (1998); Graff et al. (2013)
Trophic cascades	9 (4.2)	Positive or negative interactions spanning more than two trophic levels. Plants mediate these interactions through changes in their resource offer (e.g. chemical composition) to herbivores that in turn affect their predators.	Harri et al. (2008); Laws and Joern (2013)
Shared defense	1 (0.5)	Positive interactions occurring when a palatable beneficiary is protected by a nearby unpalatable species with adaptations to repel herbivores.	Vanderberghe et al. (2009)

tion, (2) trophic cascades, (3) apparent competition, (4) indirect mutualism via interference, and (5) indirect mutualism via exploitation. This framework characterizes indirect effects in terms of the mechanisms involved in the interaction, but fails to describe the function played by the intervening species. Alternatively, Callaway (2007) proposed six forms of positive indirect interactions focusing on plants and on the intervening organisms: (1) herbivore mediated interactions, (2) reproductive feedback and pollinator interactions, (3) disperser mediated interactions, (4) mycorrhizae interactions, (5) microbe interactions and (6) interactions involving competing terrestrial plants. While useful, these classification systems do not allow to distinguish between multiple mechanisms that can operate simultaneously, particularly for non-trophic interactions such as plant competition or facilitation (Kéfi et al. 2012), and provide only partial depictions of the networks of conceptual effects within a community because mechanistic pathways or intervening organisms are considered,

but not an integration of both sets of elements.

The study of indirect interactions may provide important information on ecological and evolutionary processes, yet, appreciation of the full scope of their impacts is limited (Wootton 2002, Brooker et al. 2008, Allesina and Levine 2011, McIntire and Fajardo 2014). The primary purpose of this study is to summarize and contextualize the research on indirect interactions within the proposed framework as a mechanism that may contribute to the development of ecological theory. The following specific objectives were addressed using a systematic review: (1) to identify the geographic and ecosystem extent of indirect interactions in terrestrial ecological communities; (2) to summarize the information on the number of trophic levels studied when examining indirect interactions in different ecosystems; (3) to determine whether the frequency of indirect interactions varies across large environmental gradients, and (4) to describe and compare the most common experimental designs and statistical techniques used to examine

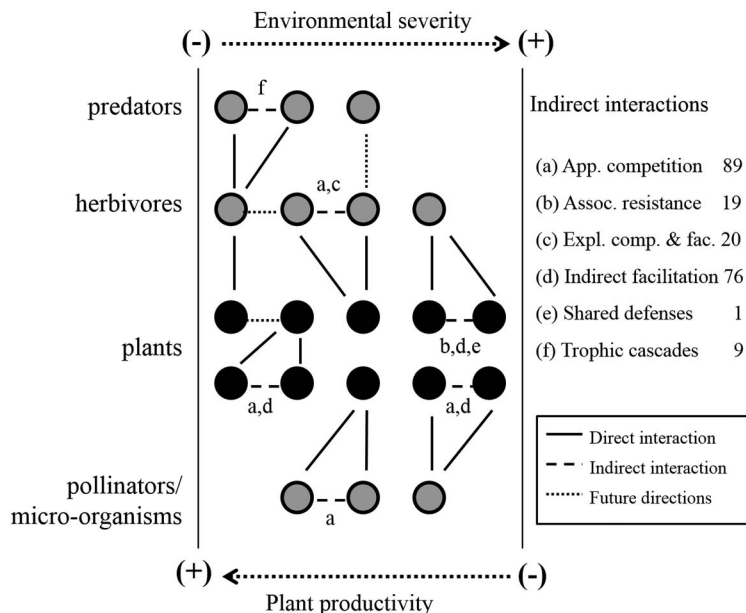


Fig. 1. Synthetic framework for indirect interactions in plant communities showing the frequency of hypotheses tested to date. This framework nests hypotheses into a trophic chain while aggregating the models of Wootton (1994) and Callaway (2007). It also depicts a hypothetical relationship where higher complexity of interactions would be supported in more productive and benign environments. Dashed lines indicate indirect effects, solid lines represent direct interactions, and dotted lines indicate future directions for studies.

indirect interactions in plant communities.

To review the recent literature (i.e., within the last 25 years) on indirect interactions, we classified indirect interactions based on a novel conceptual framework that synthesizes previous research efforts. Our framework explicitly incorporates interacting species and their hypothesized interactions both within and across trophic levels (Fig. 1) and provides a more comprehensive view of indirect interactions nested within trophic relationships. This framework includes non-feeding interactions as proposed by Kéfi et al. (2012) such as indirect facilitation or trait-mediated indirect interactions.

## METHODS

To review the field of indirect interactions in terrestrial plants we conducted a systematic review of the literature published between 1990 and July 2014 using the ISI Web of Science (WoS), Scopus, and Google Scholar. We used a combination the following keywords: “indirect”, “plant”, “interaction”, “competition”, “facilita-

tion”. The first three words were used together in combination with the last two words in separate queries (i.e., indirect\* plant\* interaction\* competition OR indirect\* plant\* interaction\* facilitation). We included literature published over the past 25 years as the study of indirect interactions is relatively young and indirect effects are clearly defined (Wootton 2002). However, we recognize the existence of previous articles examining indirect interactions even with different terminology predating this window of publications but focused on papers that clearly describe the same set of processes.

We identified 490 research articles obtained from the WoS, which were screened in order to assess their relevance. Searches in both Scopus and Google Scholar were conducted to complement the WoS search (Appendix A). The following inclusion criteria were used: (1) studies explicitly dealing with indirect interactions in terrestrial ecosystems (i.e., three or more species reported in the interaction); (2) studies describing the results of experiments specifically designed to test effects of indirect interactions versus



proposals of indirect interactions in discussion; and (3) primary empirical research reported (i.e., not reviews). Papers complying with these criteria were processed to extract data on (1) type of interaction tested; (2) number of species tested as targets, where target is defined as the species on which measurements of performance were taken; (3) role of the species involved in the interaction considering not only target species, but also species that were removed or mentioned by the authors as members of the interaction; (4) type of experiment and number of field sites; (5) type of ecosystem and geographical location of the study; and (6) type of measurements and statistical analysis performed. These characteristics provide a thorough assessment of the scope of the literature to date.

A total of 214 articles published in 53 different journals were included in this review (Appendix B). The majority of studies (49%) were published in the last 5 years (2009–2014). Two journals published several studies on indirect interactions (*Ecology*: 19%; *Oecologia*: 13%), while 28 journals published only a single article on indirect interactions for terrestrial plants.

A regression model was fit to the number of publications per year, and contingency table and chi-square analyses were used to test for biases in the distribution of the number of studies associated with particular hypotheses, geographic regions, ecosystem types, trophic structures and number of target species tested. Using the proposed framework, studies were categorized following three general categories: plant-plant, plant-animal, and plant-pollinator interactions. We included plant-pollinator interactions in a different category from plant-animal interactions because the former represents non-feeding interactions (Kéfi et al. 2012).

## RESULTS

The number of publications on this topic has increased exponentially within the last 25 years ( $r^2 = 0.78$ ,  $p < 0.01$ ). The majority of studies were conducted in the Northern Hemisphere (85%,  $\chi^2 = 105.1$ ,  $p < 0.01$ ) with a high number of publications originating from North America and Europe (Fig. 2), while indirect interactions in South America, Africa, Asia, and the tropical regions have been understudied (or at least

under-reported in the peer-reviewed literature) (Fig. 2, Appendix C). Indirect interactions have been most frequently examined in forests and grasslands (45.3% of studies), while comparatively few studies have been conducted in stressful ecosystems such as deserts, alpine ecosystems, and salt marshes (Fig. 3,  $\chi^2 = 195.1$ ,  $p < 0.01$ ).

The majority of studies on indirect interactions have focused on plant-animal interactions (70%), followed by studies dealing with plant-plant (20%) and plant-pollinator (10%) interactions ( $\chi^2 = 130.6$ ,  $p < 0.01$ ). Six main hypotheses on indirect interactions have been tested (Table 1). Apparent competition and indirect facilitation have been most frequently tested to date ( $\chi^2 = 195.1$ ,  $p < 0.01$ ). Apparent competition has been more frequently tested in relatively productive environments such as forests ( $\chi^2 = 46.6$ ,  $p < 0.01$ ) and grasslands ( $\chi^2 = 20.7$ ,  $p < 0.01$ ), or under high resource levels in controlled experiments ( $\chi^2 = 29.7$ ,  $p < 0.01$ ). On the other hand, positive effects such as indirect facilitation and associational resistance were not more frequently reported in less productive environments such as alpine ecosystems ( $\chi^2 = 2$ ,  $p = 0.57$ ), deserts ( $\chi^2 = 1.7$ ,  $p = 0.43$ ) and salt marshes ( $\chi^2 = 5.7$ ,  $p = 0.06$ ) (Fig. 3A).

The majority of studies dealt with two trophic levels across all ecosystem types (Fig. 3B,  $\chi^2 = 114.8$ ,  $p < 0.01$ ), but more complex studies included three levels in more productive environments such as agricultural ecosystems, forests, and grasslands (Fig. 3B). The method most frequently used was the single-target approach (37.7%,  $\chi^2 = 100.6$ ,  $p < 0.01$ ), and 75% of studies examining indirect interactions used less than five target species (Fig. 3C). There is no clear trend between ecosystem productivity and the number of target species utilized (Fig. 3C), although significantly more single-target studies were reported from agricultural systems ( $\chi^2 = 10.1$ ,  $p = 0.02$ ), grasslands ( $\chi^2 = 51.9$ ,  $p < 0.01$ ), and under greenhouse/laboratory conditions ( $\chi^2 = 22.9$ ,  $p < 0.01$ ).

Most studies were conducted in the field (75%,  $\chi^2 = 166.3$ ,  $p < 0.01$ ) and were also manipulative (73%,  $\chi^2 = 154.1$ ,  $p < 0.01$ ) (Appendix C). Single-site approaches were used in 74% of field conducted studies ( $\chi^2 = 731.8$ ,  $p < 0.01$ ), while studies reporting research from more than five

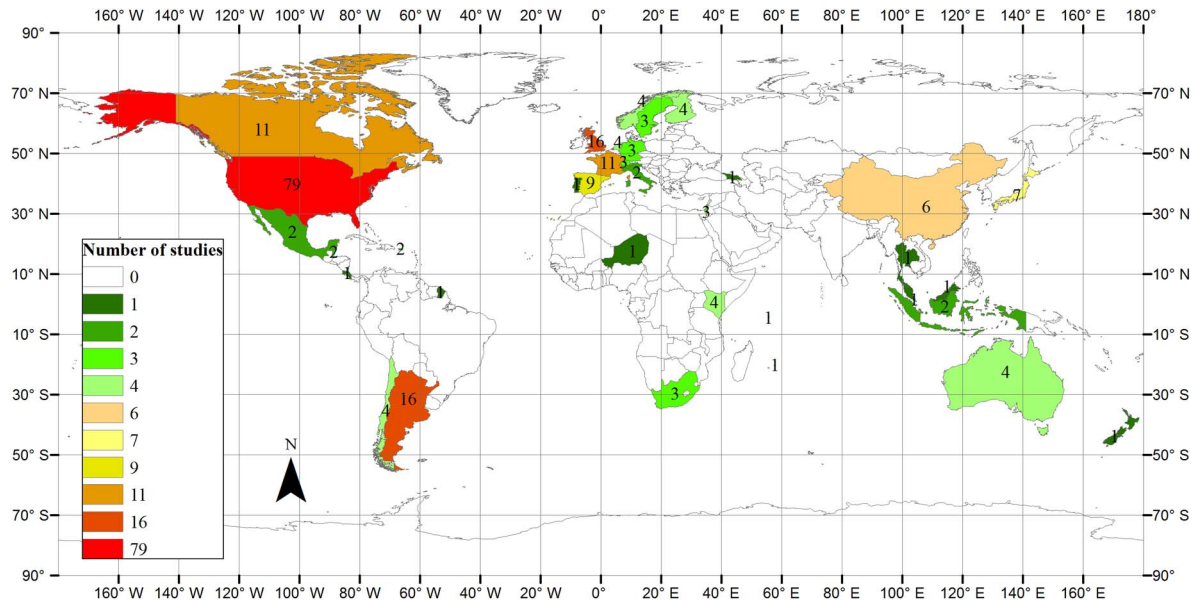


Fig. 2. Geographical distribution of studies on indirect interactions involving terrestrial plants.

field sites were particularly rare (11% of field studies). Experimental studies conducted exclusively in laboratories and/or greenhouses represented 15% of the total articles analysed in this review.

## DISCUSSION

Indirect interactions are very frequent mechanisms and can play an important role in the coexistence of species and in promoting species diversity (Brooker et al. 2008, McIntire and Fajardo 2014). Indirect interactions provide stabilizing effects within communities when they co-occur with and influence direct interactions with opposing effects (Berlow 1999), or within intransitive interacting species networks (Miller 1994, Levine 1999, Allesina and Levine 2011). Indirect interactions occur at multiple trophic levels producing higher complexity than in single trophic levels thus also affecting ecosystem functioning (Duffy et al. 2007). The influence of indirect interactions can thus scale from population to ecosystem-level impacts.

This systematic review is the first to formally synthesize the literature on indirect interactions in terrestrial plant communities, providing a quantitative summary of the scope of published research on the topic to date. Despite the

potential limitations of knowledge synthesis tools such as publication bias or the “file drawer problem” (Fanelli 2012), this review has allowed us identifying the major research gaps in this field and provides directions for future research.

First, we showed a clear geographic and ecosystem bias, with the majority of studies being conducted in North America and Europe, and in mesic ecosystems, consistent with trends found for ecological research in general (Martin et al. 2012). Indirect interactions have, however, been reported in most geographic regions and ecosystems in the world, and new studies from regions and ecosystem types that have been under-examined can provide important insights into the mechanisms and processes underlying indirect interactions. In particular, tropical and arid environments provide excellent opportunities for research on indirect interactions, as they maintain high biodiversity, their evolutionary speed is high compared to temperate regions (see Hillebrand 2004, Ward 2009), and they are important determinants of global biogeochemical processes (Millennium Ecosystem Assessment 2005).

The organizational framework proposed in this study (Fig. 1) effectively contextualized the current state of research through an explicit visualization of all logical pathways of indirect

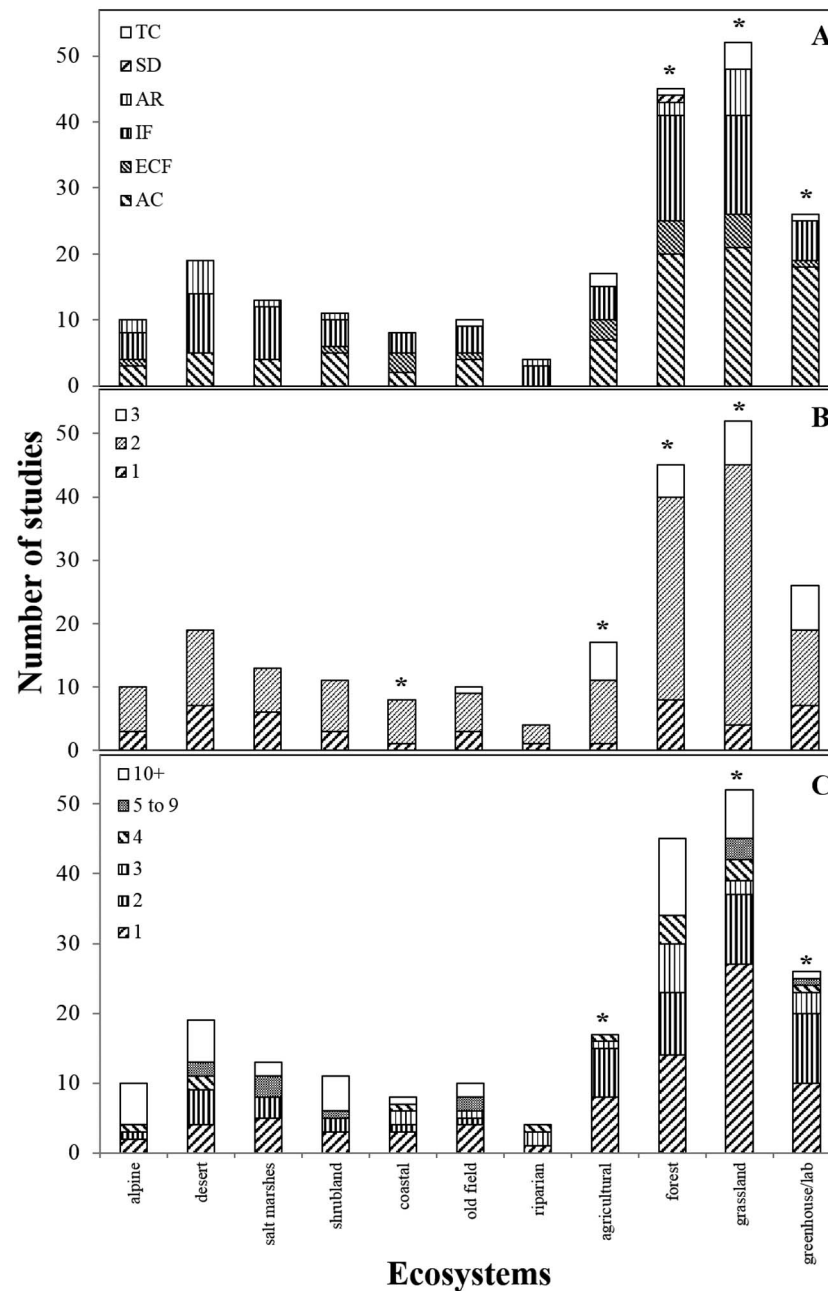


Fig. 3. Distribution of studies according to ecosystem type: (A) type of interaction tested (trophic chain (TC), shared defense (SD), associational resistance (AR), indirect facilitation (IF), exploitative competition of facilitation (ECF), and apparent competition (AC)); (B) number of trophic levels studied; (C) number of target species tested. Asterisks (\*) denote significant differences between groups ( $p < 0.05$ ).

interactions occurring in plant communities. This allowed us to pinpoint specific pathways that have received considerable attention within the literature to date. The majority of studies have

examined plant-animal feeding interactions to test hypotheses including apparent competition between plants mediated by a common consumer (Burger and Louda 1994, Recart et al. 2013)

and positive effects that result from herbivore protection, such as associational resistance or shared defenses (Vandenberghe et al. 2009, Graff et al. 2013). Studies dealing with interactions exclusively among at least three plant species are relatively scarce (21% of the studies analyzed). These interactions at the base of the trophic structure have the capacity to influence overall plant diversity (Tielbörger and Kadmon 2000, Cuesta et al. 2010) and community composition by mitigating the effects of strong competitors and facilitating coexistence in networks of competing plants (Callaway and Pennings 2000, Schöb et al. 2013). Plant-pollinator interactions have received the least attention (ca. 10% of studies analyzed) and have mainly tested hypotheses of plant-plant facilitation through shared pollinators (Johnson et al. 2003, Moeller 2004), although negative effects between invasive plant species and native species have also been tested (Morales and Traveset 2009, Gibson et al. 2012). New research efforts should address the reported gaps and focus on indirect effects exclusively among plants and on non-feeding interactions such as plant-pollinator effects taking into consideration the main pathways identified within the organizational framework in order to design more comprehensive studies.

Less studied interactions include indirect effects mediated through plant phenotypic plasticity (i.e., trait-mediated indirect effects) in response to two or more herbivores (Kaplan et al. 2011), or even more complex effects scaling-up in the trophic chain to predators (Harri et al. 2008, Laws and Joern 2013). Plastic responses of plant species to multiple environmental factors or other species have been demonstrated to be prevalent on natural communities (Werner and Peacor 2003, Miner et al. 2005), hence their incorporation on studies of indirect interactions is critical. Plasticity adds a new layer of complexity to the study of indirect interactions as different phenotypes may interact in a different way with other species (Abrams 1995, Utsumi et al. 2010). Tracking the effects of plasticity scaling-up in the trophic chain to herbivores and predators (Fig. 1) can be accomplished by studying different populations across the range of the target species or by manipulating environmental conditions in order to extend the limits of plastic responses. Plastic responses can be either

beneficial or costly to the target plant, given that one herbivore or other plant may increase or decrease the interaction with a subsequent herbivore or plant (Valladares et al. 2007), and this should be accounted for in further studies.

Plant local adaptation can also influence indirect effects given that different genotypes may interact differently with other plants or herbivores, which also have important evolutionary consequences by altering the pattern of fitness interactions between genotypes (Biere and Tack 2013). The incorporation of local adaptation to indirect interactions studies is crucial for the development of evolutionary theory as it might be responsible of co-evolutionary processes, additional spatial and temporal variation and ultimately affect the strength and direction of natural selection (Fordyce 2006). Moreover, intra-specific variability, either as a result of plasticity or different genotypes derived from local adaptation, should be incorporated into indirect interactions studies because of its ecological consequences (see Aschehoug and Callaway 2014), and also because of its evolutionary consequences. The latter are built upon the amount of genetic variability and how this is transferred vegetatively to other individuals, or sexually to the next generations.

Studies reporting negative indirect effects were more frequent in mesic environments, while studies reporting positive indirect effects in extreme ecosystems too limited in empirical scope to explore the opposite trend. This nonetheless provides partial support for the stress gradient hypothesis (Bertness and Callaway 1994), which postulates that positive effects should be more common under highly stressful biotic or abiotic conditions, while competitive interactions should be more common in relatively more benign environments. A viable set of hypotheses is that more complex chains of interactions should be supported in more benign and productive environments given that more resources are available to spread through the trophic chain, or that indirect effects resulting from non-feeding interactions with a lower energetic cost (e.g., herbivore protection, pollination) should be more frequent in less productive or more stressful ecosystems (Fig. 1). Testing these hypotheses requires more information on indirect interactions in regions and ecosystems



that have been under-examined to date. The assessment of the conditionality and context-dependence of indirect interactions will require testing indirect interactions along regional and environmental gradients, and thus developing studies to be undertaken at multiple sites.

Research on indirect effects may have been limited by difficulties in testing the mechanisms that may be involved in these interactions (Callaway 2007) and that specific literature on the design of experiments aimed at examining indirect interactions is relatively scarce. Strauss (1991) proposed the following two basic designs to assess indirect interactions: (1) removal or exclusion experiments that manipulate species with supposed strong effects in the community, and (2) construction of artificial communities using density as a variable to determine non-linear responses. The first design, the most commonly used to date (e.g., Callaway and Pennings 2000, Tielbörger and Kadmon 2000, Cuesta et al. 2010), has the limitation of assessing only the effects of the removed or excluded species at their naturally occurring density that can be solved by manipulating that factor (second design) or by replicating the experiment in different years. Importantly, the majority of these approaches used are to date based on a relatively restricted number of target species, usually one. This highlights the need for multiple target-species designs to better examine networks of interactions common in all communities, as even weak effects of species interactions might be important for the structure of naturally occurring assemblages (Berlow 1999). New protocols that include removals or exclusions embedded in the manipulation of other factors should be designed. Ecologists should move beyond the single-target approach and consider the proposed framework as a model for structuring future experiments.

Because of the importance of indirect interactions as a mechanism of species coexistence and in the assembly of plant communities, the study of indirect interactions can have important implications in the control of invasive species, both in natural and agricultural ecosystems. Studies dealing with invasive species represented 18% of the publications analyzed in this review. In general, exotic species introduced outside their native range mostly experience direct interac-

tions, but also become members of large networks of resident species interacting through indirect pathways at different trophic levels (Mitchell et al. 2006). Indirect effects may play an important role in determining the successful establishment and spread of invasive plants or the resistance of native plant communities to plant invasions (White et al. 2006). The release from natural enemies has long been considered as a mechanism promoting the successful establishment of invasive species and explaining their superior performance in their non-native range (Keane and Crawley 2002; Enemy Release Hypothesis). The release from specialized herbivores could also result in the selection for an increased competitive ability in alien plants (Evolution of Increased Competitive Ability hypothesis; Blossey and Nötzold 1995, Callaway and Ridenour 2004) with positive effects on seed production. However, exotic species can also acquire new enemies that negatively impact seed production and/or seed mortality (Vanhellemont et al. 2014). Indirect interactions, such as apparent competition, may provide invasive plant species with a competitive advantage over native species (Marler et al. 1999, White et al. 2006, Orrock et al. 2008). For instance, invasive plants can indirectly outcompete natives by increasing the pressure of shared consumers on native plants (Dangremond et al. 2010, Recart et al. 2013). However, they can also contribute to the maintenance of native diversity through the reduction of consumer pressure when unpalatable invasive plants provide refuges from herbivory to native plants (Atwater et al. 2011). Competition for shared pollinators may also affect the outcomes of the introduction of exotic plants. Exotic species have been reported to reduce pollination of native plants by attracting more pollinators (Morales and Traveset 2009, Gibson et al. 2012), however at early stages of invasion, native plant communities are able to tolerate these competitive effects via changes in the plant-pollinator network (Kaiser-Bunbury et al. 2011).

The effects of invasions on higher trophic levels via increases in herbivore populations may also be important, but to date have been rarely studied (but see Lau 2013). Indirect effects have also been examined to improve our understanding of the efficacy of the use of

biocontrol agents to control invasive populations, with studies showing that the presence of alternative hosts decreased the effectiveness of biological control, while increasing the richness of a particular guild of natural enemies can reduce the density of a widespread group of herbivorous pests and increase crop yields (Cardinale et al. 2003). Overall, the importance of indirect interactions relative to direct interactions, such as resource competition, in promoting successful invasions is largely unknown (Gioria and Osborne 2014, but see Palladini and Maron 2013). Additional studies are required to examine the role of indirect interactions in promoting plant invasions and how indirect effects may be manipulated to control plant invasions.

The effects of indirect interactions may also have important implications in rangeland management. Studies dealing with this topic represented 12% of the literature included in this review, and show that the incorporation of indirect effects into management is important to develop best practices. Grazers in general, and particularly livestock, can alter plant community composition through indirect effects when palatable plants associate with unpalatable plants (Callaway et al. 2005, Graff et al. 2013), or can exert strong control on plant communities through direct and indirect effects (Beguin et al. 2011, Vesterlund et al. 2012). Future studies should address the mechanistic pathways of herbivore effects on plant communities in order to better inform management practices.

Importantly, the effects of climate change on the net outcome of indirect interactions are still largely under-explored (Brooker 2005, McIntire and Fajardo 2014) and have only been studied once in the literature included in this review (see Auer and Martin 2013). This represents a critical gap as new climate regimes will change the physiology and fitness of plants (Kirschbaum 2004, Brooker 2005), which in turn will change the intensity and importance of indirect effects as they propagate through trophic structures (Woodward et al. 2010). Moreover, the potential effects of other global changes, such as changes in nutrient cycling and fragmentation, on indirect interactions should be examined to develop better models projecting future community composition and ecosystem functioning.

## CONCLUSIONS

Here, we proposed a synthetic framework that allows for a more readily characterization of direct and indirect effects within networks and encourages more effective examinations of causality. This synthetic framework can then be used for the interpretation of the available literature, the design of new studies and the development of ecological theory improving our ability to understand species interactions by better addressing all the players within an ecosystem together rather than in isolation. Overall, this framework is an important contribution to the literature as it identifies dominant pathways of indirect effects, assists in the determination of relevant players and casual relationships in a network of interactions, and highlights the importance of interactions at the plants trophic level as they drive the dynamics of plant communities and ecosystems.

The most frequently studied indirect interactions to date were consumer-mediated indicating that non-feeding interactions such as plant trait-mediated interactions, interactions within networks of competing plants, and trophic cascades need to be incorporated into research in this field. Experimental approaches were also relatively limited because studies commonly used single target species and single study sites. Incorporating multiple study sites along regional and environmental gradients will allow for a better understanding of the context-dependency of indirect interactions, as well as the potential effects of plasticity and adaptation of plant species on indirect interactions. By complementing this systematic review with a conceptual framework illustrating all possible interaction pathways, a number of gaps were identified and recommendations for future studies on indirect effects were made. Even for the most studied consumer-mediated interactions, additional information on their relationship with environmental gradients is required and can be important to predict the effects of global changes on the direction and intensity of indirect interactions. Future studies should also assess the relative importance of indirect interactions in comparison to that of direct interactions. If environmental conditions have the potential to alter competitive hierarchies or physiological/

phenotypic responses between interacting plants (Brooker 2005) or even at higher trophic levels, an improved understanding of their effects and scope in a wide range of biomes represents a critical step forward to predict community responses to global change drivers and develop appropriate strategies to maintain ecosystem services perhaps capitalizing on networks of interacting species.

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## SUPPLEMENTAL MATERIAL

## APPENDIX A

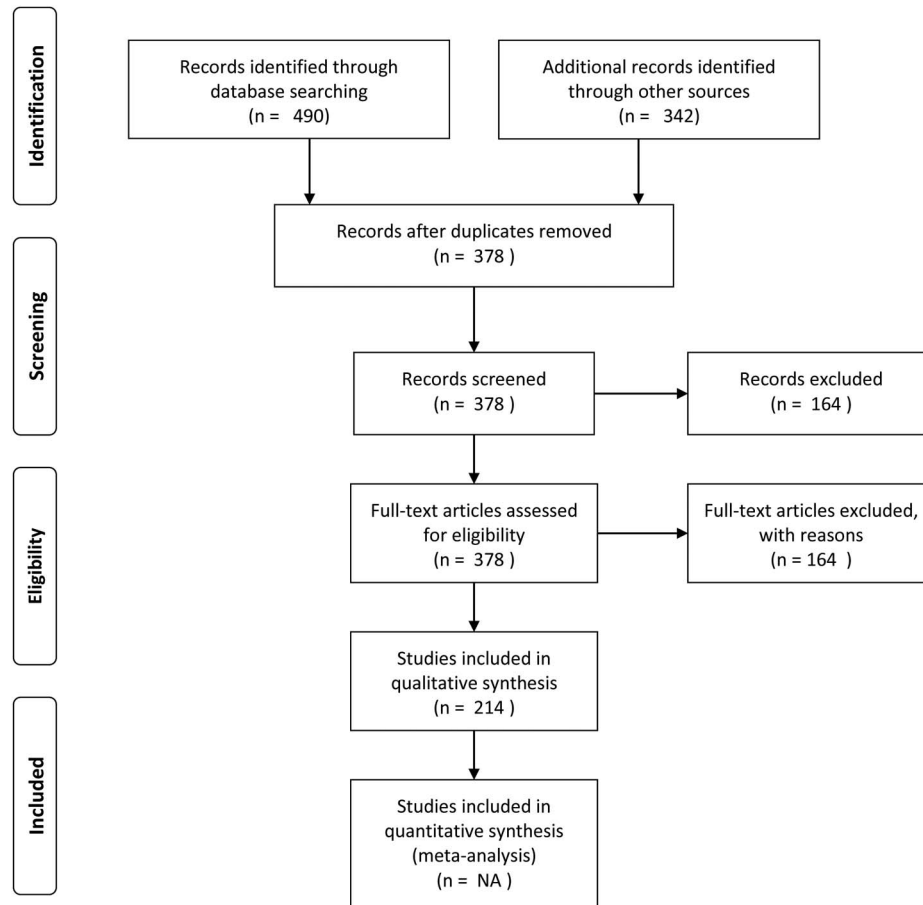


Fig. A1. PRISMA flow diagram for the identification of studies included in this systematic review (after Moher et al. 2009).

## APPENDIX B

### List of research articles considered in this systematic review

- Abdala-Roberts, L., J. C. Berny-Miery Teran, K. A. Mooney, Y. B. Moguel-Ordonez, and F. Tut-Pech. 2014. Plant traits mediate effects of predators across pepper (*Capsicum annuum*) varieties. *Ecological Entomology* 39:361–370.
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## APPENDIX C

Table C1. Summary of findings for the indirect plant interactions literature, including hypotheses tested and information about experimental procedures, target species and field sites.

Hypotheses tested†	N (%)	Experimental approach (%)‡	Experimental setting (%)§	No. target species	Geographical region¶	Ecosystem type#
Apparent competition	89 (41.6)	MN (78.7), MS (15.7), B (5.6)	FL (59.6), GL (25.8), B (14.6)	1–248 (several)	AF, AS, CA, EU, NA, OC, SA	AG, AL, CO, DE, FO, GR, GL, OF, SM, SH
Indirect facilitation	76 (35.5)	MN (65.8), MS (23.7), B (10.5)	FL (85.5), GL (7.9), B (6.6)	1–21 (several)	AF, AS, CA, EU, NA, OC, SA	AG, AL, CO, DE, FO, GR, GL, OF, RP, SM, SH
Exploitative competition and facilitation	20 (9.3)	MN (75), MS (15), B (10)	FL (75), GL (10), B (15)	1–4 (several)	AS, EU, NA, SA	AG, AL, CO, FO, GR, GL, OF, SH
Associational resistance	19 (8.9)	MN (73.7), MS (15.8), B (10.5)	FL (100)	1–34 (several)	AF, EU, NA, SA	AL, DE, FO, GR, RP, SM, SH
Trophic cascades	9 (4.2)	MN (66.7), MS (22.2), B (11.1)	FL (77.8), GL (22.2)	1–4 (several)	EU, NA, SA	AG, FO, GR, GL, OF
Shared defenses	1 (0.5)	MN (100)	FL (100)	4	EU	FO

† See text for more details on hypotheses tested.

‡ Experimental approach: manipulative (MN), mensurative (MS), both (B).

§ Experimental setting: Field (FL), Greenhouse/Laboratory (GL), both (B).

¶ Geographical region: North-America (NA), South-America (SA), Central-America (CA), Europe (EU), Asia (AS), Oceania (OC), Africa (AF).

# Ecosystem type: agricultural (AG), alpine (AL), coastal (CO), desert (DE), forest (FO), grassland (GR), greenhouse/laboratory (GL), old field (OF), riparian (RP), salt marsh (SM), shrubland (SH).