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MECHANISMS AND CONSEQUENCES OF FACILITATION IN PLANT COMMUNITIES

Functional assessment of animal interactions with shrub-facilitation complexes: a formal synthesis and conceptual framework

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Summary

1. Facilitation studies focus primarily on plants often neglecting the extended effects that cascade through ecological networks. Plants interact with other organisms through consumptive effects and a myriad of non-trophic effects such as habitat amelioration or pollination.

2. Shrubs are a dominant benefactor species frequent in plant-facilitation studies but can also have direct and indirect interactions with animals. Herein, we use a systematic review to address the following two objectives: (i) to propose a conceptual framework that explores these interactions including the functional roles of the interacting species, and (ii) to quantitatively summarize the current state of this field examining effects beyond plant–plant interactions.

3. To date, a relatively limited number of studies have examined the importance of coupled benefactor-subordinate plant positive interactions with animals (79 studies in total). From this set of studies, 36 studies documented positive plant interactions generating a total of 53 independent instances of either shrub–plant–animal or shrub–animal–plant interactions.

4. These interaction pathways were evenly split between direct (49%) and indirect (51%) interactions of shrubs with animals. Hypotheses frequently tested included seed trapping, herbivore protection, magnet pollination and facilitation-mediated secondary seed dispersal. The most common functional role of shrubs was protection from herbivory, and the most common animal role associated with plant-facilitation complexes was that of a consumer.

5. None of these studies explored bidirectional plant–animal interactions, used a network approach to describe the interaction sets, nor contrasted interaction strengths. Multitrophic, integrated sets of experiments incorporating plant facilitation into community dynamics are thus critical in advancing management of high-stress ecosystems wherein positive interactions are commonly reported.

Key-words: animals, basal facilitation, direct interactions, herbivory, indirect interactions, pollination, positive interactions, protection, seed dispersal, seed trapping

Introduction

Facilitation in plant communities is ubiquitous. This set of positive interactions typically describes benefit to at least one of the partners in the complex (Stachowicz 2001), and research focuses almost exclusively on pairwise interactions (Verdú & Valiente-Banuet 2008). Experiments on plant facilitations rarely explore bidirectional interactions (McIntire 2014; Schöb *et al.* 2014), whilst exploration of the capacity for benefactor plants to scale to other trophic levels has only recently begun (Kéfi *et al.* 2012; Baiser, Whitaker & Ellison 2013). Nonetheless, the widespread extent of positive interactions strongly suggests that biodiversity at many scales can be mediated by basal facilitation, that is positive interactions between plants that include the dominant plant species and are at the base of food or interaction webs (McIntire & Fajardo 2014). The effects of facilitation between plants are well reviewed,

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clearly indicating that facilitation functions in many ecosystems (Callaway 2007; Brooker *et al.* 2008; Filazzola & Lortie 2014) from relatively benign (Holmgren & Scheffer 2010) to highly stressed (Callaway 2013; Molina-Montenegro *et al.* 2013). However, the consequences of plant facilitation in mediating interactions with other taxa within an extended community (i.e. plants and animals for instance) remain a profound research opportunity for ecologists.

Shrubs are often a dominant plant growth form within communities and very commonly used to study facilitation. Due to their canopy and capacity to introduce significant differences in heterogeneity within communities/vegetation (Pugnaire & Haase 1996; Moro *et al.* 1997; Gomez-Aparicio *et al.* 2004), shrubs are the ideal basal species/benefactors to explore the value of positive interactions on other taxa. The mechanistic pathways associated with facilitation have also been very widely studied in shrubs (Filazzola & Lortie 2014). Shrub effects are not, however, limited to other plant species, and these effects do not disappear from systems simply because ecologists examine only the shrub–plant interactions. Shrubs can provide refuges for animals (Milchunas & Noy-Meir 2002), perches for dispersal (Hollander, Wall & Baguley 2010; Bennett *et al.* 2011; Albornoz *et al.* 2013) and resources in many forms to insects (Carmona-Diaz & Garcia-Franco 2009; Woods, Jonas & Ferguson 2012) to name only a few. These effects are likely mediated by the plant-facilitation consequences often linked to shrubs. We propose that coupling these positive plant complexes with studies of animal and insect functional interactions for shrubs is a highly tractable approach to advance ecological studies from pairwise to comprehensive networks.

Shrubs are also important agents of change in arid and semi-arid ecosystems and can both mediate anthropogenic impacts on these ecosystems (Gomez-Aparicio *et al.* 2004; Gómez-Aparicio 2009; Kleinhesselink, Magnoli & Cushman 2014) and respond independently of other species to perturbations (Gross *et al.* 2013). Direct and indirect interactions of plants and animals with shrubs are likely important considerations for management and for predicting sensitivity of these communities to change (Verwijmeren *et al.* 2013). Here, we use the literature to date on basal plant facilitation with shrubs and animals to examine the following objectives: (i) to develop a conceptual framework for interaction sets that includes positive shrub–plant–animal and shrub–animal–plant pathways and (ii) to map the main hypotheses, the most frequent interactors (animal type) and the main ecological mechanisms. This synthesis was thus formally structured to incorporate studies that examined shrub facilitation with other plant species and at least one animal species.

Conceptual framework

We need to extend positive plant interactions to other taxa and beyond pairwise interactions for several reasons. First, plant communities are ecological networks (Verdú & Valiente-Banuet 2008), but in high-stress ecosystems, benefactor (or foundation) species and the associated species often provide the nonrandom structure that predominantly shapes the community (Verdú & Valiente-Banuet 2008; Ferenc, Liu & Mike 2009; Kissling & Schleuning 2015). Consequently, benefactor plant species or nurses can generate a highly connected network of interactions not only with other plants but also with other species and thus serve as an anchor for biodiversity (Kissling & Schleuning 2015; Simanonok & Burkle 2014). Secondly, the 'nested assembly' of benefactors and beneficiaries (i.e. the benefactor and its beneficiary plant species function as a tightly coupled complex) is important because other species can use the dominants such as shrubs in very different ways from the associated beneficiary species but both sets of interacting plant species are needed to maintain the extended ecological networks (Bascompte *et al.* 2003; Memmott, Waser & Price 2004; Kéfi *et al.* 2012; Lever *et al.* 2014). Finally, nestedness generates asymmetrical communities (Bascompte *et al.* 2003; Bascompte, Jordano & Olensen 2006; Eklof *et al.* 2013) comprised of species with different sensitivities to perturbation (Memmott, Waser & Price 2004; Ferenc, Liu & Mike 2009) and a high frequency of indirect interactions (Berlow 1999; Berlow *et al.* 2009). Hence, an effective conceptual framework to capture the importance of plant facilitation must include indirect interactions, more than one trophic level, and routinely measure the plant–plant interactions that provide the catalyst for subsequent community structure.

Studies of positive plant–plant interactions and direct dominant plant effects on animals or insects are extremely useful in many systems and contexts, but to advance theory, studies that use these complexes to examine sets of interactions will more rapidly develop our understanding of the scope of facilitation. The magic number is three so to speak – shrub, annuals and animals, for instance – as a first step in shifting to network ecology. We propose two dominant pathways for shrub-facilitation systems: 'shrub–animal–plant' interactions (direct shrub effects on other taxa/animals) and 'shrub–plant–animal' interactions (indirect shrub effects on other taxa mediated through other plants; Fig. 1). Admittedly, these two pathways are more challenging studies to execute than pairwise contrasts, but there are sufficient studies conducted to date with shrubs (see below in systematic review results) to suggest that both pathways are tractable and have significant ecological implications for many important sets of hypotheses (Fig. 2). Within the direct interaction pathways, shrubs typically provide habitat, a perch, or trap and aggregate seeds for animals (Fig. 1, left panel). The animals then disperse seeds, decompose and deposit material, or due to the shrub effect, consume the beneficiary plants associated with the complex. Hence, this interaction set can be comprised of both positive and negative interactions depending on the functional role of the animal in the community (Fig. 2 for a simplified list of animal roles). Within the

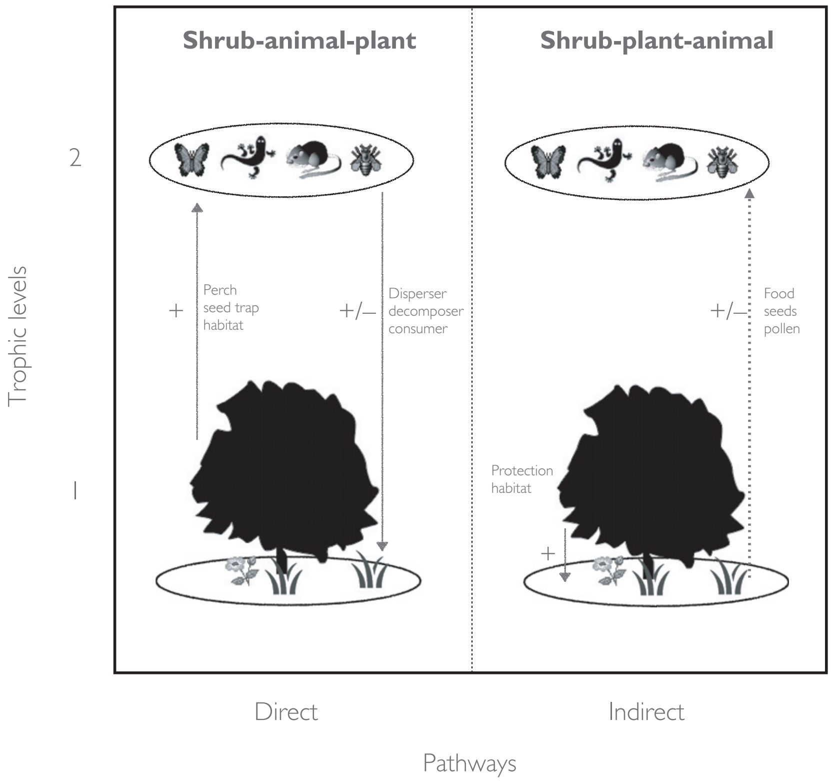

Fig. 1. A conceptual framework illustrating the interaction pathways associated with shrubs, other plant species and animals in plant-facilitation studies. Two pathways are illustrated herein – direct and indirect interactions between shrubs and animals. Direct refers to shrub–animal interactions in the left panel, whilst indirect refers to shrub–animal interactions mediated through the understorey plant species within the shrub canopy shown in the right panel. Within each panel, the interactions 'read' from left to right. The other axis separates trophic levels into those primarily focused on plant–plant dynamics (i.e. one level) and those scaling to animals (i.e. two or more trophic levels).

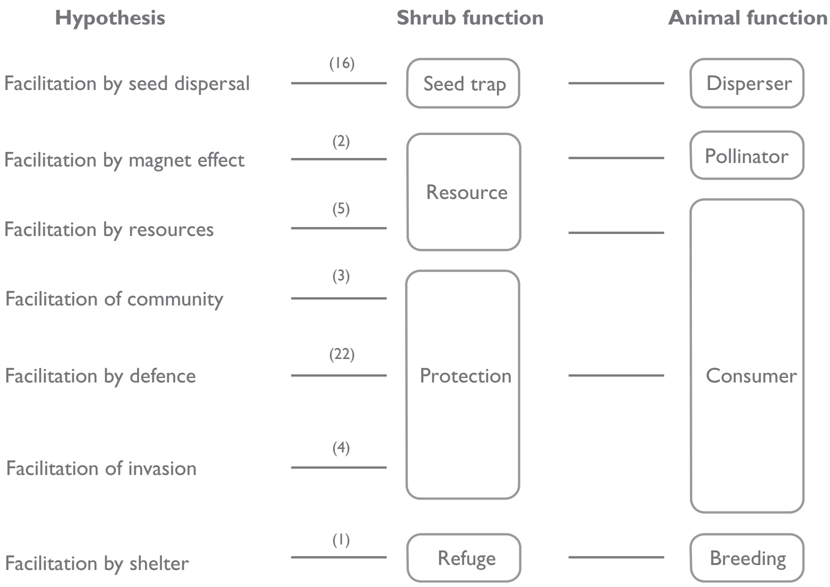

Fig. 2. A functional mapping of the hypotheses, shrub functions and animal functions associated with shrub-facilitation studies. Facilitation hypotheses are coded by primary author-reported purposes from field studies. The number of instances testing each hypothesis is listed on the first set of connection/mapping lines. Shrub and animal functions are classified in this review *post hoc* using the results reported by the primary authors (and are mapped here irrespective of statistical significance reported within primary studies). Larger rectangles denote greater coverage of a function.

indirect interaction pathways, shrubs provide habitat and protection (frequently from herbivores) but for the beneficiary plant species, and the animals then differentially consume plant material, disperse seeds of the beneficiaries, or collect and disperse pollen (Fig. 1, right panel). These complexes model direct-plant interactions and indirect shrub–animal interactions and are also comprised of positive and negative interactions dependent on both animal and shrub function (Fig. 2) and encompass the complete set of non-hierarchical, unidirectional effects derived from a nested assembly of positive interactions with shrubs.

The functional mapping of benefactor shrub species onto animal functions within extended communities in these ecosystems highlights the importance of connectance between benefactor plants and other taxa. A conceptual map of the hypotheses described in these field studies suggests that shrub and animal functions are well paired in their ecological function (Fig. 2). At least seven facilitation hypotheses have been examined in the ecological literature using plant–plant interactions and animals and describe a total of four major functions for shrubs including seed trap, resource (fruit, nutrients, etc.), protection (for both animals and other plants) and refuge/habitat for breeding specifically (Fig. 2, number of instances listed on left connector line). There are many more studies for each of these hypotheses that examine direct shrub–animal interactions ignoring plant facilitation (Herrera & Pellmyr 2002; Vázquez *et al.* 2009), but this set of studies indicates that a nested assembly approach to these systems is a viable and important tool. Ideally, these studies can also incorporate quantitative trait-level analyses to explore the context dependency of the functional role of the animals in mediating plant facilitations (Butterfield & Callaway 2013; Maron, Baer & Angert 2014). Interestingly, animal function mapped very broadly onto four of the seven facilitation hypotheses primarily functioning as a consumer (Fig. 2, right column of functions). This suggests that plant facilitation can have important linkages to food web theory development (Kéfi *et al.* 2012). The protection provided by shrubs is the dominant shrub–plant–animal functional mechanism in generating plant facilitation in these studies (i.e. accounts for 50% of the instances listed in Fig. 2). Nonetheless, a very novel implication of this mapping of animal function onto plant facilitation is that numerous feedbacks also likely emerge from these positive effects including differential foraging of herbivores under shrubs to avoid predation from higher trophic-level consumers (Kotler, Brown & Hasson 1991) and indirect interactions between understorey plants including attractant-decoy effects (Ruttan & Lortie 2014). Animals can also have positive effects including secondary dispersal and pollination, and these functions also comprised a significant proportion of reported instances of interactions with plant-facilitation complexes (Fig. 2, disperser and pollinator roles). The high degree of conceptual consilience described here demonstrates that the pathways, roles and hypotheses can be leveraged to examine many forms of facilitation.

Materials and methods

SYSTEMATIC REVIEW

A set of systematic literature searches were done in October 2014 using Web of Science with the following search terms: 'plant AND facilitat* AND shrub AND insect', 'plant AND facilitat* AND shrub AND animal', 'plant AND facilitat* AND shrub AND bird' and 'plant AND facilitat* AND shrub AND mammal'. Search results were refined by the 'ecology' category, and there were no biases associated with publication year, journal or article type (cursory inspection of distribution across journals and time indicated even representation). The remaining articles were compiled into a single list, and duplicates were removed providing a total of 79 primary research publications. We then processed each individual paper in full and excluded articles that were reviews, that did not include plant–plant facilitation complexes in some form or that did not include quantitative documentation of an interacting animal species. Each of the three authors reviewed a subset of the total articles, but we also verified each of the classifications applied by the others to ensure replicability (Cote & Jennions 2013). Supplemental searches were conducted on Google Scholar and Scopus using the same search criteria to ensure that we accurately and effectively captured the salient literature for this specific topic. A set of additional searches was also added to ensure that grazing studies that also measured plant facilitation were included.

The facilitation pathway (i.e. direct shrub–animal positive effect or mediated through the beneficiary plant species described in the conceptual framework below, Fig. 1) and associated available shrub traits were also recorded for each instance from within studies. The interaction sets were classified by interaction (direct/indirect), the pathway, shrub function, animal function and the hypothesis tested. Shrub species and any other functional attributes reported were also recorded. Additional landscape characteristics were recorded for every instance in each study including GPS coordinates, elevation, country and climate based on the six major environmental classes from the Köppen climate classification (Michalet *et al.* 2014). If coordinates were not listed, we used Google Earth to determine the location. We collected the shrub traits most associated with potential animal pathways including thorniness, shrub height, palatability and taxonomy (Soliveres *et al.* 2014). These traits were extracted directly from the papers when reported or retrieved from online data bases for plant traits, that is listed for each instance (Lortie, Sotomayor & Filazzola 2014). Thorniness was classified on a binary scale, and palatability for vertebrates was coded into one of the three following categories: palatable, unpalatable and toxic. Multiple shrub species examined within a publication were treated as independent instances. Mean annual precipitation (MAP) was derived from the WORLDCLIM data base (Hijmans *et al.* 2005). Aridity was calculated using location, MAP and mean annual temperature (De Martonne 1926).

DATA ANALYSIS

Differences in the relative frequencies of study for each major factor in this literature data set were tested with contingency table analyses (Simpson 1951; Friendly 2001) – not as a means to examine the strength of evidence nor vote count (Koricheva & Gurevitch 2013) but to ascertain and identify broad patterns in study approaches (Lortie 2014). The effect of aridity on shrub functional role was examined with a logistic regression (Stoltzfus 2011), and a general linear model was used to compare heights by functional roles (Nicholls 1989). The phylogenetic relationships for the shrub species used to examine facilitation and animals were extracted from a previously constructed phylogeny for plant species (Webb & Donoghue 2005). The shrub species belong to 12 different families and had members from both the Magnoliophyta and Pinophyta groups. The simplified phylogeny of plant species was produced using the Phylomatic software via the taxa2phylomatic function (package ECODATATOOLS) in R (R-Development-Core-Team 2014), and the shrub functional role was subsequently assigned to each appropriate node on the tree. To determine whether certain taxa were more associated to a specific role, we compared the phylogenetic α- and β-diversity of the shrub species assigned to each role to a null model (Kembel *et al.* 2010). Using the ses.mpd and comm.phylo.cor functions (package Picante), we compared the mean pairwise distances (MPD) for the within- to the between-functional role groupings, respectively. Models were run for 999 randomizations using a null model that randomized across all species within the data matrix.

Results: systematic review

A total of 79 studies were returned using the keyword search terms (described in Materials and methods). Of these, 36 studies were included in the study population used for synthesis (Table 1, Fig. S1 (Supporting information)

Table 1. A list of facilitation studies examining interactions between shrubs, other plants and animals. For full list of search terms used in this systematic review, see Materials and methods. A total of 77 articles were returned in searches, 34 studies were appropriate, and 47 independent instances reporting plant facilitation including animals were summarized in this review. The direct/indirect classification was assigned based on the shrub–animal interactions

Study authors	Shrub species	Animal interactor	Pathway	Interaction
Carlo & Tewksbury (2014)	*Celtis pallida, Prosopis velutina*	Birds	Shrub–animal–plant	Direct
Smith & McWilliams (2014)	*Viburnum recognitum, V. dentatum*	Birds	Shrub–animal–plant	Direct
Catorci *et al*. (2012)	Variety of shrub species	Large mammals	Shrub–animal–plant	Direct
Grau *et al*. (2012)	*Vaccinium myrtillus*	Insects	Shrub–plant–animal	Direct
van Zonneveld, Gutierrez & Holmgren (2012)	*Porlieria chilensis, Baccharis vernalis*	Mammals	Shrub–plant–animal	Direct
Woods, Jonas & Ferguson (2012)	*Lespedeza cuneata*	Insects	Shrub–plant–animal	Indirect
Sasal & Suarez (2011)	*Berberis buxifolia, Schinus patagonica*	Insects	Shrub–plant–animal	Indirect
Aragon & Woodcock (2010)	Variety of shrub species	Cattle	Shrub–animal–plant	Direct
Chaneton, Mazia & Kitzberger (2010)	*Discaria articulata*	Insects	Shrub–plant–animal	Indirect
Maher, Hobbs & Yates (2010)	Variety of shrub species	Large mammals	Shrub–plant–animal	Direct
McCusker, Ward & Brawn (2010)	Variety of native shrubs, *Lonicera* spp.	Birds	Shrub–plant–animal	Direct
Watling & Orrock (2010)	*Lonicera maackii*	Birds	Shrub–plant–animal	Indirect
Battaglia *et al*. (2009)	*Morella cerifera*	Birds	Shrub–plant–animal	Indirect
Carmona-Diaz & Garcia-Franco (2009)	*Malpighia glabra*	Insects	Shrub–plant–animal	Indirect
Iponga, Milton & Richardson (2009)	*Acacia erioloba, Acacia tortilis*	Large mammals	Shrub–plant–animal	Indirect
Seymour (2009)	*Acacia erioloba*	Large mammals	Shrub–plant–animal	Indirect
Farris & Filigheddu (2008)	*Rubus ulmifolius, Crataegus monogyna, Rosa canina, Prunus avium, Erica arborea*	Large mammals	Shrub–plant–animal	Indirect
Milton *et al*. (2007)	*Acacia tortilis, Prosopis* sp.	Birds	Shrub–plant–animal	Indirect
Rafferty & Lamont (2007)	*Acacia pulchella, Banksia attenuata, Banksia menziesii, Bossiaea eriocarpa, Corymbia calophylla, Hakea prostrata, Hardenbergia comptoniana, Mirbelia dilatata, Oxylobium lanceolatum*	Mammals	Shrub–plant–animal	Indirect
Duarte *et al*. (2006)	*Baccharis uncinella, Pinus elliotti, Myrceugenia euosma, Araucaria angustifolia, Baccharis mesoneura*	Mammals	Shrub–plant–animal	Indirect
Tecco *et al*. (2006)	*Pyracantha angustifolia, Condalia montana*	Birds	Shrub–plant–animal	Indirect
DeWalt, Denslow & Ickes (2004)	Unreported canopy	Insects	Shrub–plant–animal	Indirect
Garcia & Obeso (2003)	*Ilex aquifolium, Taxus baccata*	Large mammals	Shrub–plant–animal	Indirect
Verdu & Garcia-Fayos (2003)	*Juniperus sabina*	Birds	Shrub–animal–plant	Direct
Holl (2002)	Unlisted – multiple	Birds	Shrub–animal–plant	Direct
Chambers (2001)	*Artemisia tridentata*	Mammals	Shrub–plant–animal	Indirect
Holl *et al*. (2000)	*Calophyllum brasiliense, Prunus annularis, Quercus oocarpa*	Birds	Shrub–animal–plant	Direct
Maron & Jefferies (1999)	*Lupinus arboreus*	Insects	Shrub–animal–plant	Direct
Schmidt & Whelan (1999)	*Cratagus* spp.	Birds	Shrub–animal–animal	Direct
Maron & Connors (1996)	*Lupinus arboreus*	Insects	Shrub–animal–plant	Direct
Verdu & Garcia-Fayos (1996)	*Pistacia lentiscus*	Birds	Shrub–animal–plant	Direct

(continued)

Table 1 (continued)

Study authors	Shrub species	Animal interactor	Pathway	Interaction
Sommaggio, Paoletti & Ragusa (1995)	Unlisted – multiple	Insects	Shrub–animal–plant	Direct
Vieira, Uhl & Nepstad (1994)	*Cordia multispicata*	Birds and large mammals	Shrub–animal–plant, shrub–plant–animal	Direct/indirect
Gill & Marks (1991)	*Cornus racemosa, Rhamnus cathartica, Rhus typhina, Rubus allegheniensis*	Birds	Shrub–animal–plant	Direct

for flow diagram of eligibility decisions & Appendix S1 for full citations), and all records were screened and then read in full for predefined eligibility criteria (Moher *et al.* 2009). The primary exclusion criterion was 'did not include an estimate of either plant–plant or plant–animal interactions'. Other exclusions included qualitative comparison of animal or plant communities, spatial associations measured and review articles with no primary data. This generated a list of 54 independent shrub–plant–animal or shrub–animal–plant interactions (Table S1, Supporting information) using a total of 55 unique shrub species to examine plant facilitation (Table S2, Supporting information). The studies of shrub facilitation, other plants and animals were distributed globally (Fig. 3). However, studies in arid/semi-arid ecosystems and in the USA primarily comprised shrub-facilitation studies for this specific topic (contingency table analysis, $\chi^2 = 135{\cdot}3$, $P = 0{\cdot}0001$, d.f. = 72, 44% and 33% of frequencies, respectively, Fig. S2 (Supporting information) for plot). Within this literature, two trophic levels were consistently/uniformly examined (never higher-order interactions) but with a wide range of animal interactors from insects to large mammals (Table 1). The most common interactor was birds comprising 40% of all interactions in total with shrubs and associated plant species described (Table 1, Fig. S3 (Supporting information) for plot). Nonetheless, the two pathways developed in the conceptual framework significantly differed in their relative frequencies of detection of different animal interactors (contingency table analysis, $\chi^2 = 20{\cdot}1$, $P = 0{\cdot}0005$, d.f. = 4) with shrub–animal–plant interactions primarily driven by birds and shrub–plant–animal interactions driven by an even representation of birds, insects, large mammals and mammals (Fig. 4). Direct and indirect interactions were relatively reported evenly in total at 49% direct and 51% indirect (Table 1). The conceptual framework (Fig. 1) effectively classified 47 of 53 independent instances (i.e. 89% of all shrub–animal–plant and shrub–plant–animal interactions were simple interaction sets with either direct or indirect interactions between shrubs and animals, Table 1). As proposed, shrub–animal–plant

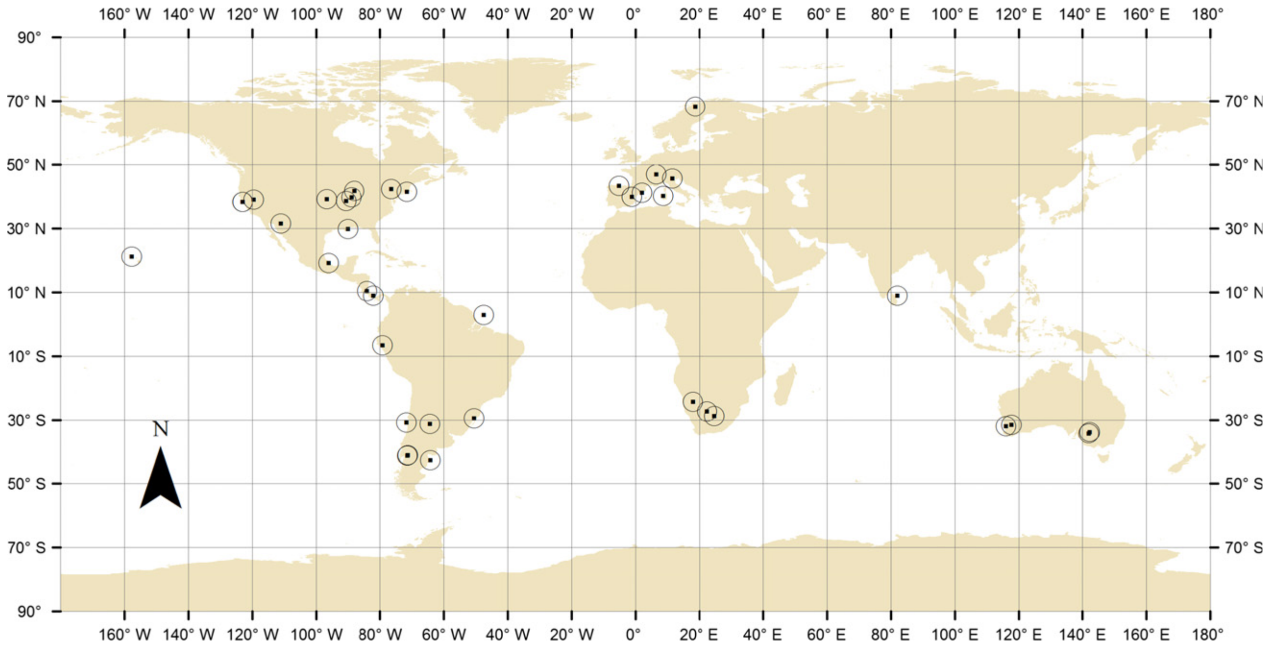

Fig. 3. A map of shrub-facilitation studies including other plant species and animals. Overlapping rings denote multiple instances of shrub facilitation within a specific region.

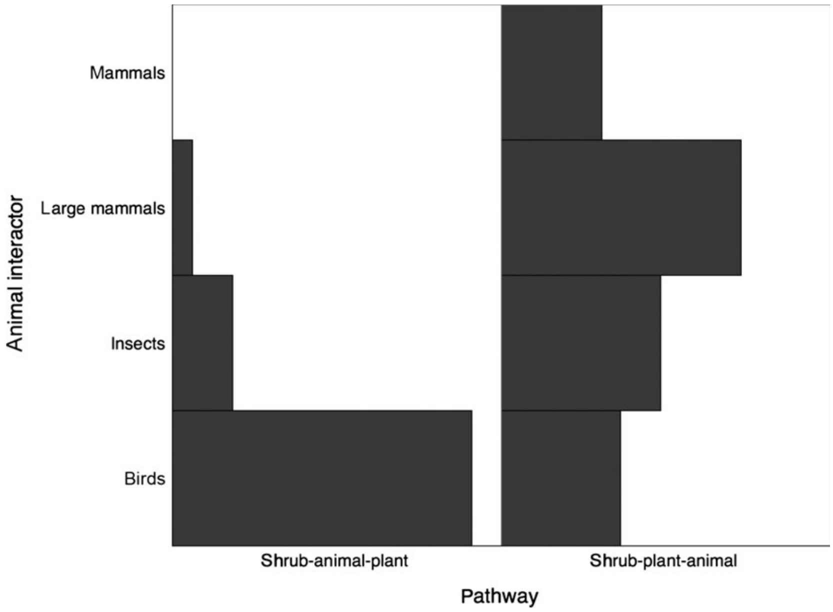

Fig. 4. A contrast of shrub-facilitation studies with other plants and animals by the two dominant pathways developed in the conceptual framework in this review. Frequency histograms plotted for each independent instance for each pathway from the systematic review data set. Independent instances for the set of interactions plotted from all studies included in review.

interactions comprised the majority of direct interactions whilst shrub–plant–animal comprised the majority of indirect interactions (contingency table analysis, $\chi^2 = 32{\cdot}2$, $P = 0{\cdot}0001$, d.f. = 1, 76% and 95% of frequencies, respectively). The remaining instances reported shrub–plant interactions and also recorded animal interactions with either the shrub or the understorey/associated plant species and were classified accordingly but did not necessarily follow a clear and coupled sequential pathway as described in the framework above. None of the instances included bidirectional interactions, costs to shrubs or more extended sets of interactions (Table 1).

The two dominant facilitation hypotheses using shrubs, associated plants and animals included protection by shrubs and facilitated secondary dispersal for both shrub and animal functional roles (Fig. 5, contingency table analyses, $\chi^2_{\text{shrub functional role}} = 157$, $P = 0{\cdot}0001$, d.f. = 25; $\chi^2_{\text{animal functional role}} = 113$, $P = 0{\cdot}0001$, d.f. = 15). Not surprisingly, in both instances shrubs primarily functioned as shelters or seed traps and animals as consumers or dispersers (Fig. 5). Even these two sets of functional roles also mapped onto other ecological hypotheses for facilitation including catalysts for community assembly, facilitated invasion by exotic species and enhanced resources (Fig. 5). The relative aridity of a site also inversely predicted the likelihood that the shrub functional role was facilitation by protection (i.e. in the most arid sites, shrubs provided shelter from herbivores but not in the least arid sites, logistic regression, $\chi^2 = 4{\cdot}92$, $P = 0{\cdot}026$).

The presence of thorns and palatability did not significantly relate to the frequency of the shrub functional roles (contingency table analysis, $\chi^2_{\text{thorns}} = 3{\cdot}8$, $P = 0{\cdot}6$, d.f. = 5; $\chi^2_{\text{palatability}} = 13$, $P = 0{\cdot}5$, d.f. = 15). Shrub heights did not differ between the reported functional roles for the shrubs (GLM, $F = 0{\cdot}8$, $P = 0{\cdot}55$, d.f. = 5, 49). There was also no obvious phylogenetic clustering of shrub species by the shrub functional roles (Fig. S4 (Supporting information) for plot), and these phylogenetic distances were not significantly different from an at-random population draw ($P = 0{\cdot}76$). The mean phylogenetic distances did not differ between groups ($P = 0{\cdot}24$). Collectively, this indicates that the genetic differences within shrub functional roles are equal to the dispersion between shrub functional roles.

Discussion

Positive plant interactions are important not only to community ecology theory but also to many other disciplines including functional ecology (Butterfield & Callaway 2013), food webs (Kéfi *et al.* 2012) and restoration (Padilla & Pugnaire 2006; Gómez-Aparicio 2009). Herein, we explored the capacity for studies using shrubs and plant facilitation to influence other trophic levels. We also furthered the concept of nested assemblies of facilitation (Verdú & Valiente-Banuet 2008) using a conceptual model and mapped the functional roles of shrubs and animals in this literature data set. The first formal objective of this synthesis was satisfied by the conceptual framework proposed because it effectively described the majority of independent instances that used shrubs to explore basal facilitation with other plants and with animals indicative of a foundational role for shrubs in many ecosystems. The functional mapping of hypotheses and shrub versus animal roles also confirmed that shrubs are well connected to the dynamics of extended ecological communities through positive interactions. The second formal objective to determine the extent that research to date supports a pivotal role for shrubs and facilitation in examining extended communities was tested using a systematic review. The global distribution of studies, a balanced frequency in examining direct vs. indirect interactions and a diversity of functional roles tested unequivocally support the interpretation that

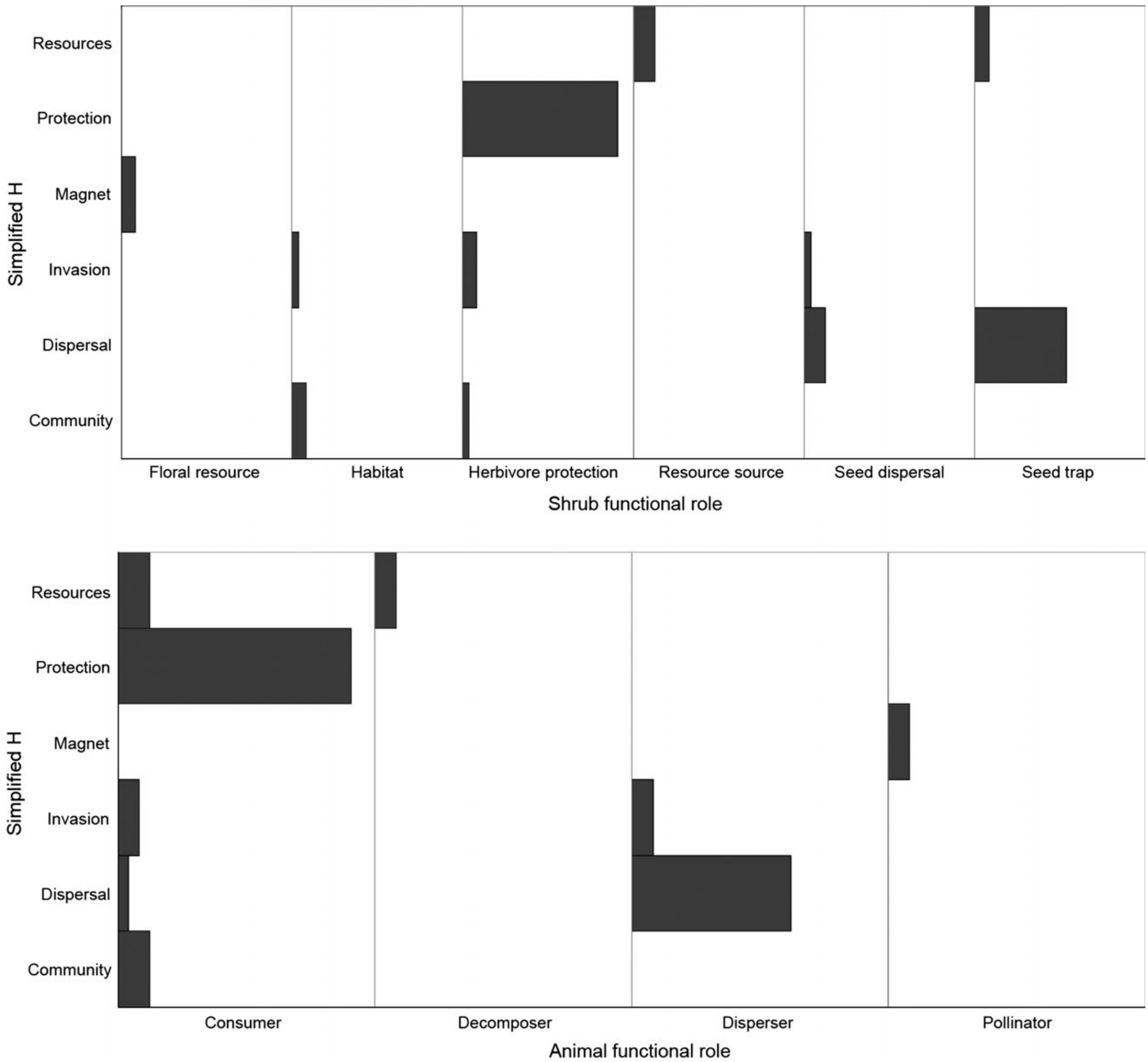

Fig. 5. The simplified hypotheses tested in basal shrub-facilitation studies that included other plant species and at least one animal species by shrub functional role and animal functional role. Independent instances are plotted as frequency histograms, and coding of hypotheses and roles was done *post hoc* in this synthesis not by the authors of primary studies.

shrub facilitation is a key research nexus between plants and animals in both functional and community ecology disciplines because facilitation mediates interactions with other trophic levels. Nonetheless, it was evident that there are at least several gaps in research examining these basic networks. Mutualisms or reciprocal-positive interactions can occur within each pathway (Bronstein 2009) and amplify the importance of foundation species in high-stress systems (Berlow 1997; Lavorel 1999). Shrubs also provide resources to animals not just to the beneficiary plants (Carlo & Tewksbury 2014), and interactions can be bidirectional (Holzapfel & Mahall 1999; Schöb *et al.* 2014). The use of plant-facilitation complexes is thus a key element to study community assembly – particularly in stressed systems.

Shrub and animal functional roles mapped well onto a wide range of facilitation hypotheses. However, the phenotype of shrubs can also respond to environmental variation (much as the interactions described above vary by context) and this adds another layer to the complexity of foundation species impacts on the structure of communities at different trophic levels (Aschehoug & Callaway 2014). The conceptual figure could thus have a space and time dimension capturing both the biotic and abiotic variations inherent in the dynamics of many ecological networks. This can be expanded to trait-mediated interaction webs (Utsumi, Kishida & Ohgushi 2010) at different trophic levels and has evolutionary implications for both the shrubs and the interacting animals (Fordyce 2006). Trait-mediated indirect effects are ubiquitous in nature

(Werner & Peacor 2003; Miner *et al.* 2005). Evidence for trait-based plant facilitation was recently reviewed, and it was concluded that the important functional traits identified in that synthesis will likely be 'idiosyncratic' at best in predicting interactions with herbivores (Butterfield & Callaway 2013). Previous research on thorns in particular indicated that variation in this functional trait can have important effects on plant–animal interactions within species (Gowda 1996). However, there were no significant patterns in shrub functional traits across studies in this review suggesting the following gaps: that variation in functional traits of the shrubs must be measured in detail within each study to be able to detect patterns (i.e. that the within-species plasticity is important) and that there is also flexibility in the functional roles and likely associated trait set variation in the interacting animal species. Collectively, mapping the frequency of functional traits onto the frequency of positive shrub interactions with plants and animals provides a powerful and novel test of the stress-gradient hypothesis such as the capacity to partition net interactions between plants not only by climate (Michalet *et al.* 2014) but also by biotic filters. The link between specific shrub traits and direct versus indirect pathways is also a new and intriguing idea; that is, a shrub trait can have a direct effect on other plants but concurrent indirect effects on animals. These new ideas are not explored to date in this literature, but the framework and review supports the value of using basal facilitation by shrubs as a mainstay for empirical functional trait development.

Phylogenetic signature analyses of interactions are another important innovation in plant-facilitation studies (Valiente-Banuet *et al.* 2006; Valiente-Banuet & Verdu 2007; Verdú *et al.* 2009). In this review, the shrub phylogeny did not cluster by the functional role. However, it was not uncommon for related species to share functional roles in interacting with animals because of analogous traits. Members of the Proteaceae family such as *Banksia menziesii*, *Banksia attenuate* and *Hakea prostrata* were all identified as reducing herbivory for other plant species (Rafferty & Lamont 2007). Members of the same family can have similar trait sets such as thorns as an adaptation to the arid environments they inhabit (Flores & Jurado 2003; Hanley *et al.* 2007). Other unrelated species shared similar functional roles simply because of the environment they co-inhabit. There are also instances of exaptation in conifers in this data set that shared functional roles of facilitation (i.e. seed dispersal and habitat use facilitated by traits likely evolved for other purposes) in temperate climates where consumer pressure and resource availability were not as limiting relative to arid ecosystems (Flores & Jurado 2003; Filazzola & Lortie 2014). Importantly, a single set of traits can function non-exclusively through different pathways. For instance, the *Acacia* genus is a thorny shrub species that reduced herbivory for plants in their understorey (Rohner & Ward 1997) but has also been shown to encourage seed dispersal because birds used them as a perching site (Milton *et al.* 2007). Given that each shrub functional role had a diverse set of associated shrub species, it is reasonable to suggest that any one species can positively interact with other plants and animals through multiple roles. This finding implies that many shrub species can generate different pathways to facilitation not just 'key' shrub types. There is likely no benefactor archetype for all other plants and animals. This is does not necessarily challenge the notion that many facilitative interactions are species specific but that as previously proposed, experimentation should explore this topic in depth (Callaway 1998). In this review, only one study reported a single shrub species acting simultaneously through two different functional roles (Vieira, Uhl & Nepstad 1994). Consequently, this indicates that both shrub specificity and experimental designs that incorporate measures of multiple interaction pathways will be productive in describing the capacity for positive interaction sets to map onto multiple functional roles for other species including animals.

Conclusions

Shrub–plant–animal and shrub–animal–plant facilitations are largely unexplored and only as simple sets of interactions. None of these studies explored reciprocal plant–animal interactions, used a network approach to the study facilitation, estimated cost to benefactors nor contrasted interaction strengths. We propose that integrated sets of experiments incorporating plant facilitation into community dynamics are thus critical in advancing management of high-stress ecosystems and advancing theory development in community ecology more broadly. Shrubs are an excellent foundation species to catalyse this research, and associated animals functioning as consumers or dispersers are also likely to significantly mediate interactions. Environmental gradients and more comprehensive trait sets – particularly for the shrubs – should be incorporated into plant-facilitation studies to address community-level responses to perturbation. The frequency of plant–animal interactions and trait-mediated facilitation is a novel extension to existing theory.

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Data accessibility

Data set examining functional assessment of animals with plant-facilitation complexes has been deposited in figshare: http://dx.doi.org/10.6084/m9.figshare.1489525 (Lortie *et al.* 2014). This contains a full list of studies detailing the exclusion criteria, the primary topic explored within each listed study, detailed classification and coding of every study included in the systematic review (describing the functions, measures and hypotheses tested) and the traits as listed for the dominant shrub studies from the included studies.

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Supporting Information

Additional Supporting information may be found in the online version of this article:

Fig. S1. PRISMA flow diagram for identification and exclusion criteria of studies included in this review on shrub facilitation, other plant species and animals.

Fig. S2. A contrast of studies examining shrub facilitation with other plants and animals by country.

Fig. S3. The relative proportion of animal interactors with shrub–plant–animal or shrub–animal–plant facilitation nested assemblies.

Fig. S4. A phylogeny of shrub species by shrub functional role from the systematic review on shrub facilitation, other plants and animals.

Table S1. A list of the instances from each study testing facilitation with shrubs that included both other plants and animals (see Materials and methods for full list of search terms) summarized here.

Table S2. The shrub traits from each study testing facilitation with shrubs that included both other plants and animals (see Materials and methods for full list of search terms) summarized here.

Appendix S1. The full list of studies used in systematic review on shrub facilitation, other plants and animal complexes.