

RESEARCH
REVIEW



A systematic review and conceptual framework for the mechanistic pathways of nurse plants

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ABSTRACT

Aim To conceptualize the mechanistic pathways of the nurse-plant syndrome by life-form and to identify the implications of positive plant–plant interactions for landscape and evolutionary ecology.

Location Global.

Methods We conducted a quantitative review examining 298 articles to categorize the literature on nurse-plant interactions based on geographic region, mechanism of facilitation, ecological hypothesis and nurse life-form.

Results A total of nine different nurse mechanisms were identified and two were classified as meta-mechanisms. We found that shrubs were the dominant nurse life-form (46% of total studies) and that studies of positive plant interactions were most frequent in areas of high abiotic stress. Nurse-plant studies were also distributed unevenly around the globe with nearly a quarter in the South American Andes and Spain. Studies testing the direct nurse–protégé interactions were the most frequently performed, including the ecophysiological responses of protégé species (32.2%). Research gaps identified in the nurse-plant literature included indirect interactions and seed trapping as well as the large-scale implications for landscape ecology and evolution.

Main conclusions Nurse plants are often considered keystone species because they commonly structure plant communities. This is an important confirmatory finding in many respects, but it is also novel in that it challenges traditional plant ecology theory and has important implications for landscape-level dynamics over time. The categorization of mechanisms proposed provides a conceptual framework useful for organizing the research to date and can accelerate linkages with theory and application by identifying important connections. It is becoming increasingly apparent that future studies of the nurse-plant syndrome must decouple and consider multiple mechanisms of interaction to explain the processes that influence community structure, particularly in high-stress conditions, given a changing climate and potential shifts in biodiversity.

Keywords

Abiotic stress, facilitation, interactions, nurse plant, positive interactions, protégé, restoration, systematic review.

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INTRODUCTION

The inclusion of facilitation into ecological theory has generated a paradigm shift that establishes positive interactions as pivotal in explaining many of the dynamics of ecosystems (Callaway, 1995; Bruno *et al.*, 2003). An apparent core concept used to

examine facilitation is the nurse plant; these are species that benefit other plants or taxa through various mechanisms (Gómez-Aparicio *et al.*, 2004; Brooker *et al.*, 2008) and are typically perennial species such as shrubs, trees or cushion plants. With facilitation research increasing in scope and frequency (Bruno *et al.*, 2003; Brooker *et al.*, 2008), there is a growing need

Table 1 A list of ecological hypotheses tested using nurse-plant mechanisms. Each hypothesis is listed with its central concept, key associated paper and possible nurse mechanism that may be used. More than one hypothesis may be examined within a study at a time.

Hypotheses tested	Applicable nurse mechanism	Key paper(s)
<i>Mechanisms</i>		
Nurse plants directly affect the fitness or productivity of plants in their vicinity	All	Flores & Jurado (2003), Callaway (2007)
Nurse plants indirectly affect the fitness or productivity of plants in their vicinity through an intermediary species	Seed trapping, pollinator visitation and herbivore protection	Barbosa <i>et al.</i> (2009), McIntire & Fajardo (2014)
<i>Gradients</i>		
Net interactions between nurse and protégé are dependent on abiotic stressors	Substrate modification, soil moisture retention, soil nutrient modification, abiotic stress amelioration	Bertness & Callaway (1994), He <i>et al.</i> (2013)
Plant interactions mediate consumer pressures	Herbivore protection	Smit <i>et al.</i> (2006)
<i>Community assembly</i>		
Nurse plants facilitate the development of community structure to increasing complexity	All	Hacker & Gaines (1997), Raffaele & Veblen (1998)
Nurse plants alter spatial dynamics of plant communities and increase local diversity	All	Franco-Pizaña <i>et al.</i> (1995), Soliveres <i>et al.</i> (2012)
Nurse plants alter the evolutionary trajectories and phylogenetic history of beneficiary species	All	Valiente-Banuet & Verdú (2007)
<i>Applications</i>		
Nurse plants are tools for restoration of native flora in degraded landscapes	All	Gómez-Aparicio (2009)
Nurse plants mediate the invasion regimes of non-native plant species	All	Cavieres <i>et al.</i> (2007)

to clearly define nurse plants and the mechanistic pathways of their effects, particularly on other plant species. The nurse-plant syndrome can in theory affect every life-history stage of another plant species including: (1) seed dispersal by increasing the reproductive output of beneficiary species, (2) seed arrival by functioning as a seed trap, (3) seedling establishment through substrate modification, (4) increased plant growth from reduction in herbivory or abiotic stress, and (5) increased survival and reproductive output. Consequently, the result of these positive interactions on individual plants can cause community-level changes in species composition (Cavieres & Badano, 2009). Both direct (nurse–protégé) and indirect (nurse–intermediary–protégé) pathways (Bruno *et al.*, 2003) can have an impact on the various life stages and can shift in sign or magnitude with the ontogeny of a plant (Callaway & Walker, 1997). In successional contexts, the pioneer plant may facilitate the development of others and eventually be replaced as it is exceeded by the increasing size of the benefactor species (Connell & Slatyer, 1977). Though this is an excellent example of facilitation, it is not a typical nurse–protégé interaction in the way the term is used in the current literature because the nurse generally remains as a component of the ecosystem and the protégé is commonly (but not always) an annual plant species (Brooker *et al.*, 2008; McIntire & Fajardo, 2014). Nurse plants have also been tested as tools for restoration in disturbed landscapes (Zhao *et al.*, 2007; Gómez-Aparicio, 2009) and can interact with invasive plant species (Cavieres *et al.*, 2007). Nurse-plant studies have the capacity to inform both theoretical and applied plant ecology.

In a review conducted by Brooker *et al.* (2008), six key facilitation concepts were identified, and we have expanded upon

these to generate nine ecological hypotheses that are specifically tested using nurse plants (Table 1). These ecological hypotheses represent the scope of current nurse-plant topics and simplify the broad facilitation literature into distinct disciplines including practices from theoretical, applied and experimental ecology. Although positive plant interactions have been previously reviewed (Bruno *et al.*, 2003; Flores & Jurado, 2003; Callaway, 2007; Brooker *et al.*, 2008), further efforts are required to understand the ecosystem-level implications of the nurse-plant syndrome. For instance, nurse plants are capable of driving biodiversity in multiple ecosystems (McIntire & Fajardo, 2014). There is also additional evidence of nurse plants as components of landscape-level processes such as ecological succession (Raffaele & Veblen, 1998), invasion biology (Cavieres *et al.*, 2007) and as a restoration tool (Gómez-Aparicio, 2009). Therefore, a formal review and conceptual framework is needed to quantitatively summarize the current state of research on nurse plants and to anchor the mechanistic pathways to global implications for ecology. Conceptual frameworks provide a comprehensive understanding of the literature to date and set an agenda for future avenues of research. By supplementing these frameworks with a systematic review, we provide a more robust synthesis that both highlights novel pathways and identifies gaps in the research.

CONCEPTUAL FRAMEWORK

Nurse plants can positively affect members of their species as well as other plant species through a suite of direct and indirect mechanisms (Callaway, 2007). Previous studies have categorized

Table 2 A list of mechanisms associated with nurse plants. Five of the nurse–protégé interactions are from Flores & Jurado, 2003 (*) and the remainder are proposed herein. Each nurse mechanism is listed with its facilitative effect, key associated paper and categorization as a meta-mechanism. A meta-mechanism is an effect that occurs as the result of another nurse mechanism.

Nurse mechanism	Protégé response	Key paper(s)
Abiotic stress amelioration	Reduced environmental variability	Bertness & Callaway (1994), Lortie & Callaway (2006)
Herbivore protection*	Reduced browsing/trampling	Barbosa <i>et al.</i> (2009), Smit <i>et al.</i> (2006)
Pollinator visitation	Increased pollination rate	Lavery (1992)
Substrate modification*	Physical assistance	Carrillo-Garcia <i>et al.</i> (1999)
Seed trapping*	Increased seed arrival	Vander Wall & Joyner (1998); Giladi <i>et al.</i> (2013)
Soil moisture retention*	Higher soil moisture	Maestre <i>et al.</i> (2009)
Soil nutrient modification*	Higher soil nutrient	Walker <i>et al.</i> (2001)
Nurse-mediated distribution (meta-mechanism)	Nurse association	Franco & Nobel (1989), Franco-Pizaña <i>et al.</i> (1995)
Nurse-mediated evolution (meta-mechanism)	Altered genetics/phylogeny	Valiente-Banuet & Verdú (2007)

positive interactions into pathways between the benefactor and beneficiary (Anthelme & Dangles, 2012; McIntire & Fajardo, 2014). However, only one previous synthesis has examined the physical mechanisms underpinning plant–plant facilitation (Flores & Jurado, 2003). The nurse–protégé mechanisms were originally categorized into five pathways including seed trapping and safe sites for moisture, herbivory, nutrients and physical support (Flores & Jurado, 2003). However, empirical research has since progressed to extend these mechanisms to include at least two primary and two ancillary mechanisms (Table 2). For example, the physical support safe site has been expanded here to consider all forms of substrate modification including root grafts, the provision of soil humus and increasing soil microorganisms such as mycorrhiza (Cuenca & Lovera, 1992; Carrillo-Garcia *et al.*, 1999). The first additional primary nurse mechanism is the indirect facilitation of pollinator visits by magnet species effects (Feldman *et al.*, 2004; Molina-Montenegro *et al.*, 2008). A nurse may sustain a population of pollinators or may function with protégé plants to jointly increase visits of shared pollinators (Lavery, 1992; Moeller, 2004). The second additional mechanism is the amelioration of abiotic stress, such as protection from extreme weather, heat or cold – this is particularly common in studies examining the stress gradient hypothesis (Bertness & Callaway, 1994; Maestre *et al.*, 2009; Holmgren & Scheffer, 2010). The remaining two additional pathways are best classed as meta-mechanisms because they are ancillary effects that function as responses to primary mechanisms. The first meta-mechanism is nurse-mediated distribution, which affects the spatial presence of protégé plants with more frequent occurrences of species or individuals under the nurse canopy versus open microsites (Franco-Pizaña *et al.*, 1995). Commonly, this pathway uses general patterns of association and not formal spatial statistics (e.g. Franco-Pizaña *et al.*, 1995; Yang *et al.*, 2010). The second meta-mechanism is nurse-mediated evolution resulting in changes to genetics (Liancourt *et al.*, 2012), ontogenic shifts (Armas & Pugnaire, 2009) or phylogenetic variation (Valiente-Banuet & Verdú, 2007; Armas & Pugnaire, 2009; Armas *et al.*, 2013). These nine mechanisms represent the entire current documented scope of interactions of nurse plants with

other plant species (Fig. 1). Collectively, this framework organizes nurse-plant effects by life stage because net interactions in plants often shift with plant development (Valiente-Banuet & Verdú, 2008). We summarize this framework as a clock, wherein each independent notation in the ring represents a potential mechanistic pathway studied empirically, and the clockwise motion represents the progression of the protégé's life stages. The conceptual framework specifically lists key pathways of plant facilitation but also allows space for the incorporation of as yet unexamined additional pathways.

In this study, we also conducted a formal systematic review to quantitatively describe the nurse-plant literature. The primary purpose of this review is to summarize, organize and firmly link studies of the nurse-plant syndrome to ecosystem and evolutionary theory. We explored this topic by synthesizing the studies associated with the following objectives.

1. To assess the global extent of published nurse-plant effects and test whether there is a correlation between climate and the reported mechanisms.
2. To describe, contrast and highlight research gaps for each nurse-plant mechanism and ecological hypothesis including differences in the life-form of nurse plants.
3. To broaden and formalize the semantics of the nurse-plant syndrome by organizing all the studies and incorporating processes associated with evolution and macroecology (i.e. so-called meta-mechanisms).

For simplicity, we assume that publication frequency is an indication of prevalence in natural systems, but we also recognize that there are legitimate biases in the study of an ecological process associated with the viability of studying particular places, species and processes (Onwuegbuzie & Leech, 2007). We predict that resource-limited environments will have the greatest proportion of nurse-plant studies because positive interactions have been shown to be greatest in conditions of high stress (Lortie & Callaway, 2006; Maestre *et al.*, 2009) but may collapse at gradient extremes (Michalet *et al.*, 2013). Consequently, we predict that mechanisms associated with ameliorating abiotic stress and hypotheses testing these (e.g. the stress-gradient hypothesis) are more commonly studied, and studies have been increasing in frequency recently. This does not necessarily imply

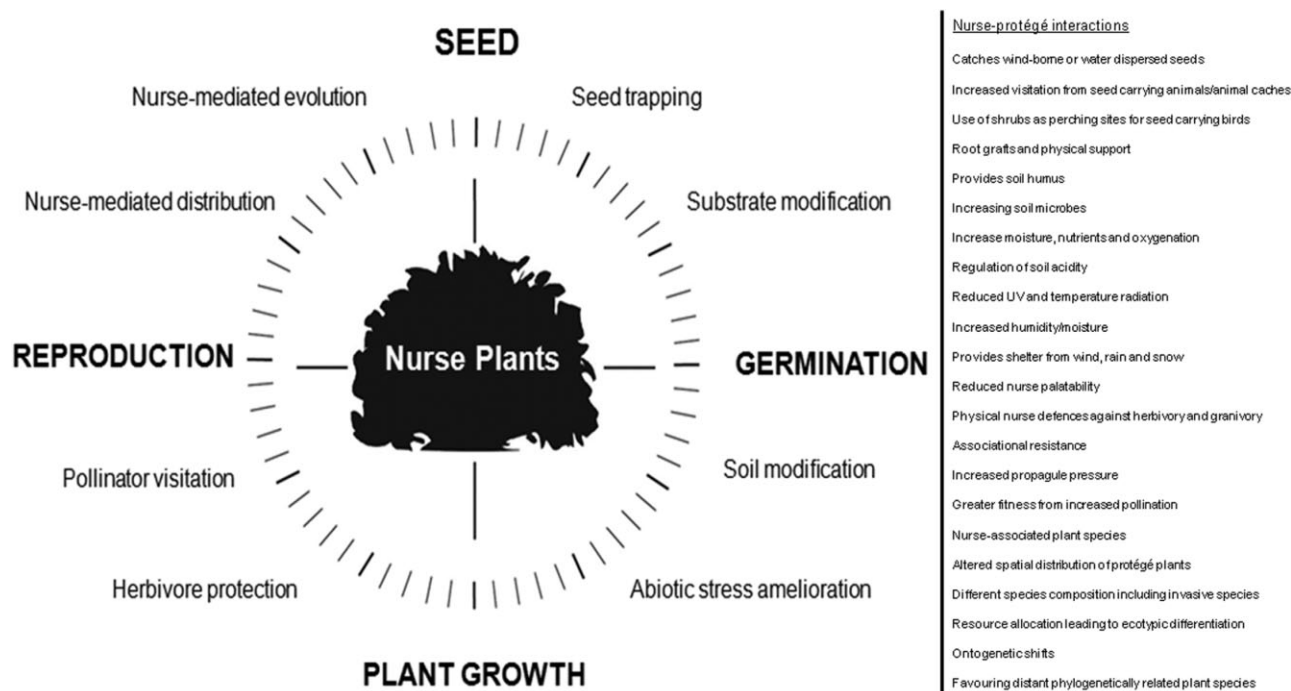


Figure 1 A conceptual framework for the abiotic and biotic mechanisms of nurse-plant effects studied in the ecological literature. Nurse mechanisms are ordered based on response of protégé life-stage and clockwise motion around figure represents the progression of a plant through its life history (i.e. seed, seedling, plant/growth, reproduction). Listed to the right are possible nurse-protégé responses.

relative importance, simply that nurse plants more commonly interact by these mechanisms. Some nurse life-forms may be particularly associated with specific mechanisms, such as shrubs with seed trapping because xeric environments have fewer physical obstructions. We also predict that nurse-protégé interactions play a dominant role in shaping the ecosystems where they are present, but have been relatively poorly studied in aspects of landscape ecology and evolution. By better understanding nurse-plant interactions we are able to project ecosystem responses to landscape-level changes and develop more effective land management practices.

METHODS

Systematic review

A systematic literature search was conducted using Web of Science from 1960 to 2014 with the following search terms: 'nurse' and 'plant*'. Topics unrelated to ecology were excluded, such as substance abuse, virology and biochemistry (Fig. S1 in Supporting Information). The remaining 560 studies were individually reviewed for relevance and then categorized based on ecological hypothesis (Table 1) and nurse mechanism (Table 2). Using the same criteria, a subset of these 560 studies was examined and classified by an independent expert on plant interactions to ensure replicability (Côté *et al.*, 2013). Publications that tested more than one mechanism or hypothesis were independently classified, i.e. an article could be associated with multiple

categories. Supplemental searches were conducted on Google Scholar and Scopus using the same search terms to ensure accurate capture of the nurse-plant literature.

The articles were then further reviewed for additional criteria that are common in nurse-plant studies, such as climate and nurse life-form, to summarize the field of research. The climate for every study site was recorded from each paper and organized into six major environmental classes based on the Köppen climate classification: tropical (megathermal), arctic-alpine, arid and semi-arid, mediterranean (mesothermal), temperate (microthermal) and other (Michalet *et al.*, 2014). The 'other' classification represents environments that belong to the previously mentioned climate categories but have been severely degraded due to anthropogenic disturbances, such as agricultural barrens or mining scrapes. Nurse plants were classified into the following life-form groups: shrub, tree, cushion, other plant life-form and inanimate object. Geographical coordinates were also extracted from each study and mapped using ArcGIS 10 (ESRI, 2010).

Data analysis

The relative frequency of each ecological hypothesis and nurse mechanism tested per study was compared using Pearson's chi-squared tests (*chisq.test* function) in R version 2.13 (R Development Core Team, 2011). Each nurse mechanism can function independently, meaning that we would expect that each should have equal relevance and similar numbers of asso-

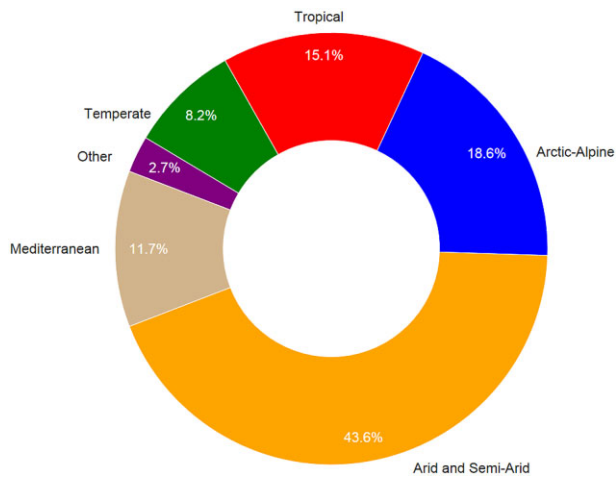


Figure 2 The percentage of nurse-plant studies conducted in each global climate.

ciated studies. We also expect that the ecological hypotheses will favour theoretical based studies rather than applied ones. To contrast the frequencies of nurse mechanisms and ecological theories, we used a Pearson's chi-squared test and compared the proportion for each grouping with the resulting standardized residuals as post hoc tests (Coolidge, 2012). To compare how the frequency of studies has been changing over time, we plotted the number of nurse studies per year for the last 20 years. Additionally, we fitted linear models with year as the predictor and each ecological hypothesis and nurse mechanisms as the response variable. We also separated the number of studies associated with each ecological hypothesis based on nurse life-form and conducted a Kruskal–Wallis test followed by post hoc multiple comparisons tests (*pgirmess* package in R). To determine if the proportion of nurse life-forms was similar between ecological hypotheses, each one was treated as a percentage of the total number of nurse-plant studies and a one-way ANOVA was conducted between life-forms. Tukey's honestly significant difference tests were used for these post hoc comparisons.

RESULTS

A total of 298 papers explicitly reported testing for nurse-plant mechanisms (Fig. S1). The largest proportion of studies (43.6%) were conducted in arid and semi-arid environments ($\chi^2 = 178.62$, $P < 0.001$, $n = 127$; Fig. 2), and the study of nurse plants was distributed broadly across the globe, but not uniformly (Fig. 3). Many studies were conducted in Spain and the Andes, representing 14.1 and 9.1% of studies, respectively (Fig. S2). A total of 57% of studies tested only one mechanism ($\chi^2 = 213.54$, $P < 0.001$, $n = 171$), and only six articles examined four or more mechanisms. There were also significant differences in the frequency of study for each nurse mechanism ($\chi^2 = 164.68$, $P < 0.001$, $n = 298$) or ecological hypothesis ($\chi^2 = 132.38$, $P < 0.001$, $n = 298$). Amelioration of abiotic stress was the most frequently documented mechanistic pathway ($n = 118$; Table S1). Pollinator enhancement and evolutionary

changes in protégés were rarely documented mechanisms and are significantly understudied (Table S1).

Hypotheses associated with documenting the direct effects of nurse-plant mechanisms were the most commonly studied ($n = 96$; Fig. 4b, Table S2). Indirect nurse-plant mechanism were significantly understudied (Table S2). Hypotheses associated with the effect of nurse plants on population dynamics and biodiversity ($n = 73$) and net interactions between the nurse plant and protégé depending on abiotic stressors ($n = 62$) were commonly studied, collectively making up 45% of the total studies (Fig. 4). The study of nurse mechanisms in general has increased dramatically in the last 20 years (mean effect \pm SE = 2.27 ± 0.42 , $t_{19} = 5.37$, $P < 0.001$; Fig. S3), driven primarily by studies that examine the amelioration of abiotic stress, increases in soil moisture and favourable modification of soil nutrients (mean effect \pm SE = 1.08 ± 0.26 , $t_{19} = 4.10$, $P = 0.0006$; Fig. S3).

There was no trend observed between a particular nurse mechanism or ecological hypothesis and a nurse life-form. Shrubs were the dominant life form in nurse–protégé interactions (46% of the total studies) and were most commonly examined for all nurse mechanisms and ecological hypotheses ($\chi^2 = 17.4$, $P = 0.001$; Fig. 4). All other nurse-plant life-forms were taken into account in a similar number of studies including trees, cushions and inanimate objects ($P > 0.05$; Fig. 4). The proportion of the nurse life-forms associated with each ecological hypothesis differed significantly ($F_4 = 27.94$, post hoc contrasts, all $P < 0.001$).

DISCUSSION

Nurse plants are important focal species for the study of plant–plant interactions, ecophysiology, restoration and the ecology of dry land ecosystems. Not surprisingly, studies in arid and semi-arid environments comprised the bulk of the literature on nurse plants. There were also relatively high frequencies of arctic-alpine and Mediterranean studies that supported the stress gradient hypothesis. Herein, the nurse-plant literature was appropriately classified based on the mechanistic pathways and ecological hypothesis examined. Specifically, studies testing for the amelioration of abiotic conditions have been increasing steadily and significantly in the last two decades. The capacity for nurse plants to facilitate protégé plants through other mechanistic pathways not associated with abiotic stress is an important research gap for future research efforts. Shrubs are the most common life-form tested to date, but there is also accumulating evidence that some tree species, inanimate objects and cushion-forming alpine species may function similarly. Importantly, these findings suggest that the mechanisms associated with shrubs are also applicable to other life-forms. Lastly, recent studies have examined the role of nurse plants in the contexts of applied ecology and landscapes. This conceptual framework clearly illustrates that nurse-plant interactions can affect all plant life stages leading to community-level changes and that these ideas have been well documented in the literature but poorly integrated as related mechanisms. Thus, this

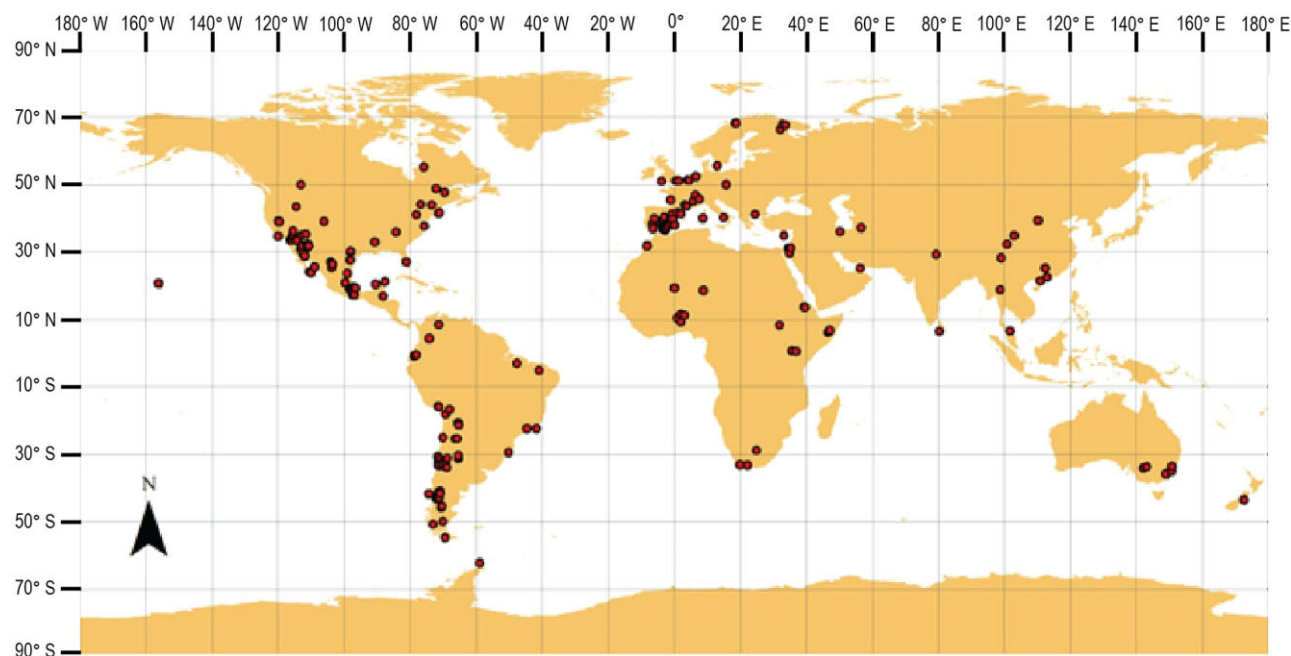


Figure 3 Geographical location of previous studies for nurse plants throughout the world.

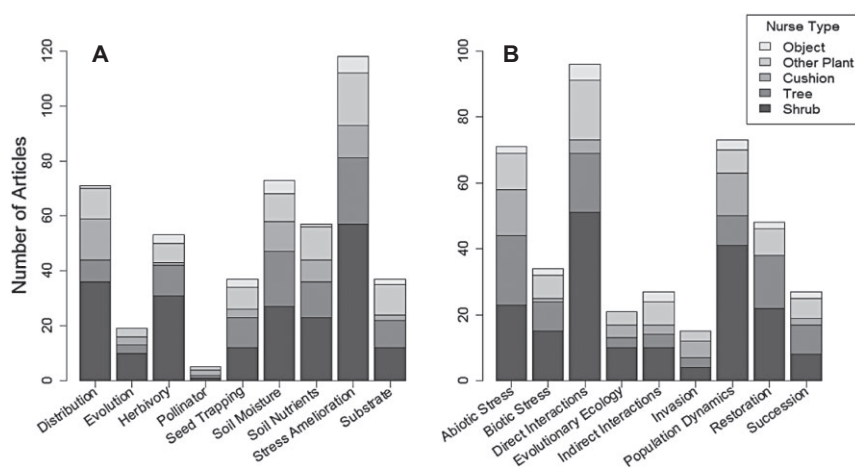


Figure 4 The number of associated studies based on nurse life-form for each nurse mechanism (a) and each testable ecological hypothesis of facilitation (b).

synthesis provides a coherent and improved description of nurse mechanisms, hypotheses and empirical studies while introducing the potential macroecological significance of nurse–protégé interactions over evolutionary time.

Global distribution of nurse-plant studies

Specific land formations in the Western Hemisphere are particularly amenable to the study of nurse plants. This could either be due to the researchers/themes preferred in those regions or the ecology of those systems. For example, 40.1% of the alpine studies were conducted in the South American Andes. The coupled effects of high plant diversity, limited biogeographical connectivity between mountains and the harsh aridity gradient of the longitudinal span of this range (Arroyo *et al.*, 1988) provided ideal conditions to document nurse-plant interactions, i.e.

similar to research reported at the edge of life (Michalet *et al.*, 2013). These elements may be important in applying the nurse-plant methodology to the study of plant–plant interactions in other systems. These climate trends were similar to the synthesis by Flores & Jurado (2003), in that nearly half of all nurse-plant studies were conducted in arid and semi-arid environments. Although experiments in tropical and temperate climates collectively comprised 25% of all studies, both are extremely broad climatic categories including a diverse range of ecosystems such as coastal systems, grasslands, forests and wetlands. Generally, nurse-plant studies are most frequently reported in climates characterized by abiotic stress (Maestre *et al.*, 2009; Holmgren & Scheffer, 2010; Malkinson & Tielbörger, 2010) or in degraded habitats for the purposes of restoration (Gómez-Aparicio *et al.*, 2004; Padilla & Pugnaire, 2006). The nurse-plant syndrome can be generally restricted to resource-limited environments though

positive interactions between plants may diminish in areas of extreme stress (Maestre *et al.*, 2009). However, a recent study in Antarctica has also shown that facilitation was important even in extremely adverse systems (Molina-Montenegro *et al.*, 2012). The high frequency of nurse-plant studies in stressful environments may explain the greater proportion of studies examining mechanisms of abiotic amelioration. Nurse plants may therefore be functioning as key drivers of community composition in these systems (Hacker & Gaines, 1997; McIntire & Fajardo, 2014). A global survey of positive interactions and climate in the alpine region found that net interactions generally shifted from negative to positive with increasing altitude, but that different climatic regions did not always respond similarly (Michalet *et al.*, 2014). Facilitation by drought-tolerant species in xeric climates increased at low altitudes thereby buffering the potential effects of climate change, but in environments with moderate-severity stress, climate change could amplify the interplay between facilitation and competition increasing the variability in community dynamics (Butterfield, 2009). In a related meta-analysis, He *et al.* (2013) also detected a shift from negative to positive interactions globally with species richness and also found that the strength of interactions varied with climate. Consequently, expanded tests for nurse plants on gradients and in more precise sets of climatic conditions are needed to better model the mediation effects of nurse plants on communities. Alternative mechanistic pathways and interactions between the different species are also critical because each will respond differently to climatic perturbations.

Research gaps in the research on nurse-plant pathways

Though indirect nurse effects have been less extensively studied than direct mechanisms, they are still important pathways of facilitation. For instance, biotic 'stress' is a major driver of plant-plant interactions (Graff & Aguiar, 2011) and nurse plants can indirectly protect understorey plants from herbivory (Barbosa *et al.*, 2009). A nurse plant can reduce the likelihood of disturbance for neighbouring plant species through shared defences by either being unpalatable (Smit *et al.*, 2006; Bee *et al.*, 2009) or by physically obstructing large animals with thorns and branches (Flores & Jurado, 2003; Callaway, 2007). More commonly, nurse plants act through associational resistance to reduce visibility to herbivores, thereby decreasing browsing events (Barbosa *et al.*, 2009). Nurse effects on external species are not always negative and may act to increase visits of species that are favourable for protégé plants. For example, visits for pollination can be indirectly increased when a nurse functions as a magnet species for protégé plants that are otherwise unattractive to pollinators (Laverty, 1992; Callaway, 1995). A nurse can also indirectly improve soil chemistry for the understorey community by facilitating mycorrhizal colonization (Cuenca & Lovera, 1992). Direct and indirect mechanistic pathways can also be specific to certain nurse species (Callaway, 1995) and not purely a physical effect such as the trapping of windborne seeds (Giladi *et al.*, 2013). For instance, apparent competition among annuals

under a shrub canopy can sometimes be reduced by nurse effects (Soliveres *et al.*, 2011; McIntire & Fajardo, 2014). Currently, these indirect pathways are ideal opportunities to better understand the impacts of intermediary species in nurse-protégé interactions. This will provide the capacity to construct interaction networks, thereby advancing the development of ecological theory (Goudard & Loreau, 2008). Direct and indirect effects may function in concert, interact nonlinearly, and influence more than one pathway simultaneously, but we commonly study only singular, direct effects in most instances.

Although not usually associated with nurse-plant interactions, seed trapping is a mechanism that can positively affect seed arrival of dispersing plant species. Seed dispersal strongly influences population dynamics thereby affecting major ecological processes including biodiversity, plant invasion and community composition (Myers & Harms, 2009). Nurse plants can increase seed arrival of protégé plants either directly, by nurses physically obstructing passing seeds (Groeneveld *et al.*, 2007; Giladi *et al.*, 2013), or indirectly through animal-mediated transport such as bird perching sites (Debussche & Isenmann, 1994) and mammal caches (Vander Wall & Joyner, 1998). Although seed trapping increases seed arrival, it may not be commonly termed a nurse-plant mechanism because the net outcome of effects on seed success may not always be positive due to increased competition, pathogens or granivory and because seed dynamics in the field are difficult to quantify (Howe & Smallwood, 1982; Lortie & Turkington, 2002). For seed trapping to function as a nurse mechanism, the increased seed arrival must result in an increased spatial correlation between nurse and protégé (Cody, 1993), and this may occur if the nurse acts to reduce seed dormancy (Franco-Pizaña *et al.*, 1996), seed granivory (Munguía-Rosas & Sosa, 2008) or act as a 'fertile island' by ameliorating abiotic conditions (Yang *et al.*, 2010; Wang *et al.*, 2011). Seed trapping is an under-examined mechanism because it is contingent on additional nurse effects to encourage positive spatial correlation between plant species (Cody, 1993; Cavieres & Arroyo, 2001). It is nonetheless a compelling and probably viable opportunity for increased precision in estimating annual plant dynamics in stressful arid and semi-arid systems that rely heavily on seed banks.

Differences in nurse-plant life-form and positive interactions

The life-form classifications of nurse plants were not specifically related to any particular mechanism or ecological hypothesis. Nurse 'objects' were the least studied life-form but often outperformed their living counterparts, probably because of an inherent lack of competition with the potential resource needs of protégé plants (Munguía-Rosas & Sosa, 2008; Peters *et al.*, 2008). It has been commonly observed that shorter seed dispersal distances are found in more heavily vegetated areas (Bullock & Moy, 2004). Therefore, it was expected that shrubs would be the dominant life-form for seed trapping in xeric environments because the annual plants communities are often sparse and highly variable in cover (Caballero *et al.*, 2008). Unexpectedly,

shrubs were not significantly more studied than other life-forms as a means of seed-trapping, potentially because secondary dispersal from rainfall deposits seeds in the sediment flows of open areas in many arid systems thereby reducing the direct effects of shrubs on seed movements (Aerts *et al.*, 2006). Shrubs, however, were the dominant life-form for protection from herbivory because their morphology (i.e. thorns, branching, woody) makes them conducive to herbivore deterrence (Callaway, 2007). Trees, cushions and other plant species may not be as physically repelling as shrubs but still deter herbivory through secondary compounds and reduced palatability (Smit *et al.*, 2006; Barbosa *et al.*, 2009; Bee *et al.*, 2009). The observed frequency of life-forms, particularly the high proportion of nurse shrubs, is also a consequence of the climates used to study this form of plant facilitation. For example, cushions are more likely to be found in arctic-alpine climates while shrubs dominate mediterranean, arid and semi-arid climates. In the literature to date the climate rather than the mechanism most commonly predicts the life-form of a nurse–protégé interaction, but this does not preclude the possibility that many other plant species can function as nurse plants in other communities.

Inclusion of two meta-mechanisms and implications for applied ecology

This review has highlighted two previously undefined meta-mechanisms that should be considered in mainstream nurse-plant theories. The first meta-mechanism is nurse-mediated evolution that occurs when the selection pressures on protégé plants are changed by the nurse plant (Michalet *et al.*, 2011). Plant traits such as biomass and fitness can be increased in stressful environments by positive interactions (Callaway *et al.*, 2002). Nurse-plant effects are temporally dependent and may result in ontogenetic shifts from facilitation to competition as the protégé plant develops, especially with increasing phylogenetic relatedness of neighbours (Valiente-Banuet & Verdú, 2008; Armas & Pugnaire, 2009; Armas *et al.*, 2013). Positive interactions may also cause ecotypic differentiation wherein plants in an ameliorated nurse microclimate are selected for competitive traits while those in an open microclimate are selected for stress-tolerant traits (Liancourt & Tielbörger, 2011). In some instances, nurse plants may also alter evolutionary trajectories by increasing the phylogenetic diversity of plant communities through the facilitation of distantly related species (Lortie, 2007; Valiente-Banuet & Verdú, 2007; Soliveres *et al.*, 2012). These positive interactions between nurse and protégé can either encourage or hinder gene flow within a plant population, thereby affecting rates of ecological speciation (Liancourt *et al.*, 2012). The second described meta-mechanism is the nurse-mediated distribution of neighbouring plant species (Franco & Nobel, 1989; Franco-Pizaña *et al.*, 1995). In stressed environments, protégés may become associated with a specific nurse plant such that the area under the nurse acts as an ‘island’ surrounded by an ‘ocean’ of uninhabitability (Walker *et al.*, 2001; Wang *et al.*, 2011). Consequently, many studies have shown that certain plant species are found to be positively cor-

related with a nurse-plant species (e.g. Franco-Pizaña *et al.*, 1995; Yang *et al.*, 2010; Wang *et al.*, 2011). This presents concerns for biological conservation because some invasive species may use nurse plants as a pathway for invasion into stressful environments that are typically unavailable to them (Cavieres *et al.*, 2007). However, the spatial associations between nurse and protégé can also have positive implications, such as introducing a nurse species to increase succession in a deteriorated plant community (Lookingbill & Zavala, 2009). Nurse plants can also function as drivers of biodiversity by increasing niche availability and creating novel habitats (McIntire & Fajardo, 2014). The inclusion of these two meta-mechanisms, nurse-mediated evolution and dispersal, are a novel categorization of studies that extends the scope of positive plant interactions and establishes important linkages with evolutionary theory.

Nurse plants have restoration applications as well as global implications for conservation biology, but their capacity to act in this way has been poorly examined. Although the research on direct nurse-plant mechanisms and ecophysiology is by no means complete, additional attention needs to be focused on the practicality of nurse–protégé interactions. Overall, there are considerably fewer papers examining applied ecological practices such as restoration ecology and invasion biology. Nurse plants have been repeatedly used for restoration purposes in a variety of degraded habitats and ecosystems (e.g. Gómez-Aparicio *et al.*, 2004; Padilla & Pugnaire, 2006). Although nurse plants are commonly applied in the reforestation of the Mediterranean Basin (Castro *et al.*, 2002), there are other potential areas applicable for landscape restoration including the lower subtropics, arid ecosystems and peatlands. The widespread potential for nurse plants to be used for restoration applications strengthens their role in applied ecology.

CONCLUSIONS

A conceptual framework was proposed herein to organize nurse-plant mechanisms by the life stages of protégé species with plant development being the most affected. The high frequency of studies in arid/semi-arid ecosystems is consistent with a former review on the topic and a clear signal that nurse plants are important in these ecosystems. The dominant pathway studied is abiotic amelioration, but there is accumulating evidence for the role of nurses as seed traps or as refuges from consumers. There was no specific relationship between particular life-forms and mechanisms or ecological hypotheses tested, suggesting that the ecological relevance of nurses can be very broad. However, climate classification was an important factor in organizing the nurse-plant literature. Two novel meta-mechanisms are also proposed that describe and incorporate the emerging empirical research on distributions and evolutionary implications for protégé species. This conceptual framework by life stage provides a unification of the nurse-plant literature to date and suggests that linkages between different mechanistic pathways will become increasingly important in facilitation studies. These nurse mechanisms may act independently or function in concert, making it critical that future

studies decouple the different pathways of facilitation when trying to understand the ecology of communities defined by nurse–protégé interactions.

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Additional references to data sources can be found at the end of Appendix S1.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site.

Figure S1 The PRISMA diagram describing the search protocol used for systematic review to refine articles to those that are relevant.

Figure S2 Frequency of previous studies for nurse plants based on degrees of longitude and latitude.

Figure S3 The total number nurse studies conducted in the last 20 years.

Table S1 The proportion of studies associated with each nurse mechanism.

Table S2 The proportion of studies associated with each ecological concept.

Appendix S1 Bibliometric synthesis of nurse-plant studies around the globe.

BIOSKETCHES

Alessandro Filazzola is a second year masters student in biology at York University in Canada. He is a community ecologist and conservation biologist with field experience developing experimental designs and applying them in practical contexts. A problem solver in using advanced statistics and biological indicators to predict trends in environmental data and developing restoration programmes. Alessandro's research includes quantifying deer browsing using plants as indicators and studying the facilitation effects of nurse plants in environments with drought stress for the purposes of restoration.

Christopher J. Lortie is an associate professor of biology and geography at York University in Canada. He is an integrative scientist with expertise in community theory, sociology and quantitative methods. Empirical research by Lortie and collaborators includes biogeographical comparisons of many forms of community dynamics including invasion, climate change, keystone species and plant–insect interactions. Research efforts include structural network analyses to couple trophic and non-trophic interactions with basal facilitation in desert ecosystems. Lortie is also a senior editor for *Oikos* and serves on other boards including *PLOS ONE*, *Journal of Ecology* and *PeerJ*.

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