Title of article: The loss of foundation species revisited

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Abstract

Ecologists and environmental scientists often prioritize research efforts with conservation importance. Dominant, widespread, or locally abundant species at low risk of extinction receive relatively little attention unless they are invasive. Native foundation species create habitats and environmental conditions that support many associated species and modulate local-scale ecosystem processes, but the generally high local or regional abundance of foundation species may lead to less research about them. We used citation analysis (2005-2014) to examine research following from a suggestion to identify and study foundation species while they were still common and not threatened. We explored the use and expanding definition of the foundation species concept, as well as the trajectory and ecological focus of research on foundation species throughout the world in 378 papers published in this nine-year span. Contemporary authors who cite key papers defining a foundation species pay little attention to its actual definition and species studied in this context rarely were identified as foundation species. Although functions and roles of foundation species, such as creating unique microclimates or supporting dependent species, are being studied, less research is focused on identifying them before they are threatened or lost from the ecosystem that they otherwise define. Invasive species were identified as the most common threat to foundation species. Our citation analysis and synthesis provides a new conceptual framework linking identification of and research about foundation species with their functional roles and our ability to manage emerging threats to them.

Key Words

Citation analysis; conservation management; foundation species; invasive species; retrospective study; threaten species.

Introduction

Ecologists and environmental scientist often rank species in order of conservation importance (Mace et al. 2007) and target for research or monitoring those species that are rare (Courchamp et al. 2006, Angulo and Courchamp 2009), endangered (Caro and Sherman 2010), or occupy habitat biodiversity hotspots (Myers et al. 2000). However, species that are dominant, abundant, or are not in immediate danger of population loss are studied less frequently by conservation biologists (Gaston and Fuller 2007).

The assumption that abundant species are not a priority for conservation is unwarranted: common species often are ecologically important as structural, dominant, or foundation species, and commonness itself is rare (Gaston and Fuller 2007). As a consequence, abundant species – and especially foundation species – may receive little attention from conservation biologists until their populations are threatened and a compelling need arises to understand their life history, their roles and functions in their ecosystem, and the factors that threaten these roles. Yet, understanding how foundation species interact with their environment and other species could allow for much better forecasts of the cascading consequences of population declines and enable early adoption of strategies to ameliorate those consequences.

Dayton (1972), working in a benthic marine system, described a foundation species as, "*a single species that defines much of the structure of a community by creating locally stable conditions for other species and by modulating and stabilizing fundamental ecosystem processes.*" In applying the foundation species concept to terrestrial ecosystems, Ellison et al. (2005) identified foundation species as (usually) primary producers that occupy low trophic levels, are locally abundant, regionally common, and create stable habitat conditions that are necessary for survival of dependent species (see also Baiser et al. 2013). The loss of foundation species can

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impact energy and nutrient fluxes (Jenkins et al. 1999), microclimate conditions (Snyder et al. 2002), food webs (Baiser et al. 2013), and biodiversity (Ellison et al. 2005, Tingley et al. 2002). Foundation species thus fundamentally shape both community structure and ecosystem function.

Other categories, such as ecosystem engineer (Jones et al. 2010), core species (Hanski 1982), dominant species (Grime 1984), and structural species (Huston 1994) describe particular aspects of foundation species (Ellison et al. 2005). However, foundation species are distinct from these other types of species because they also have unique sets of traits that are functionally irreplaceable in a given ecosystem and that, coupled with a foundation species' system-wide dominance and high abundance, define that ecosystem (Fig. 1). However, foundation species appear to be studied less than either rare species or other types of "important" species: a title-only search in Web of Science (run on 1 July 2015 for papers published between 1972 and 2014) recovered "foundation species" in only 54 papers, compared to 473 for "rare species", 202 for "dominant species", 109 for "keystone species", and 73 for "ecosystem engineer". Foundation species are not often monitored and, as with other common species, any population changes likely go unnoticed until there is a sudden or dramatic decline in their abundance or range (Gaston and Fuller 2007). For example, whitebark pine (*Pinus albicaulis* Engelm.), a foundation species in many western North American high-elevation forests, is threatened by the introduced fungal pathogen *Cronartium ribicola* (J. C. Fisch.). If this foundation tree species had been better understood when it was abundant, preventing its loss or mitigating the negative effects of reductions in its population may have been possible.

In 2005, Ellison et al. published an article in *Frontiers of Ecology and the Environment* emphasizing the importance of identifying foundation species before their populations become threatened. Ellison et al. (2005) argued that as of the early 21st

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century, understanding the consequences of foundation species loss was based on only a small number of case studies and these case studies were conducted after the species had declined. The lack of data on how foundation species, while still abundant and widespread, structured and supported ecological systems led to an incomplete understanding of their overall role in these systems. Thus, Ellison et al. (2005) also called on scientists to fill knowledge gaps on how foundation species respond to environmental changes and biotic threats. Since its publication, Ellison et al. (2005) has been cited nearly 500 times in primary articles, review articles, and book chapters; here, we ask whether these citations actually reflect increasing identification or study of foundation species.

We reviewed papers published through the end of 2014 that cited Ellison et al. (2005) and assessed whether these studies 1) adequately or accurately defined foundation species; 2) identified a particular foundation species; 3) identified an ecological role associated with foundation species; and 4) identified a threat to foundation species populations. We synthesized our results to develop a framework for studying foundation species that emphasizes how identifying and studying them can improve both our understanding of the roles of these species and our ability to manage effectively emerging threats to them.

METHODS

Data collection was restricted to a citation analysis of Ellison et al. (2005) because that review not only introduced the concept to terrestrial ecology, but also specifically addressed the importance of studying foundation species and encouraged research on them. We recognize that many other studies of foundation species have highlighted their importance, but because Ellison et al. (2005) is the

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most highly cited paper about foundation species and emphasized an agenda for future research, we were interested in whether it has acted as a catalyst for increasing research on foundation species.

Using several research platforms and article databases (Web of Science, JSTOR, Google Scholar, Pub Med), we found that Ellison et al. (2005) was cited in at least 446 papers through December 2014 (number of citations varied among the databases). We reviewed 378 of these papers to determine the main focus of the original research described and its relationship to the key questions proposed by Ellison et al. (2005). Review papers, book chapters, commentaries, and all other non-primary literature were excluded from the present study (n=47).

QUESTIONS FOR DATA COLLECTION

We developed a set of six of questions to assess research on foundation species published since 2005 and used that information to compare cohesiveness between individual studies and the goals of Ellison et al.'s. The raw data are available from the Harvard Forest Data Archive, file HF-259 (http://harvardforest.fas.harvard.edu/data-archive).

Question 1: Was a foundation species precisely or accurately defined and what definition was used?

It is important to know whether other studies recognized or differentiated foundation species from other similar, but distinct, species roles. The definition of a foundation species definition found in each paper was placed into one of five categories: 1) Ellison et al.'s (2005) definition; 2) Dayton's (1972) definition; 3) Dayton and Ellison's definitions combined; 4) neither Dayton or Ellison's

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definition (i.e., “Other”); or 5) not defined. If categorized as “Other”, then the alternative definition was recorded. If other definitions included multiple terms, each term was counted, so that a definition could be classified with multiple terms.

Question 2: Was a foundation species explicitly studied?

We recorded as a single binary variable (yes/no) indicating whether or not any single focal study species in the study was explicitly considered a “foundation species.”

Question 3: What was the main role of the foundation species that were studied?

Two broad roles of foundation species were distinguished: *direct support of other species* (*e.g.*, effects on associated species or assemblages); and *modulation and stabilization of fundamental ecosystem processes* (*e.g.*, effects on abiotic or biogeochemical processes). We classified each paper as focusing on support for associated species (“Community”), modulation/stabilization (“Ecosystem”), both, or neither.

Question 4: Were threats to foundation species identified?

We identified six broad classes of threats to foundation species: “climate change” (*e.g.*, changes in atmospheric composition, temperature, or hydrological flow): “invasive species” (*i.e.*, nonnative or invasive species); “habitat degradation” (*e.g.*, pollution, habitat loss, human disturbance,); “exploitation” (*i.e.*, over-use by humans or increased herbivory or predation by non-human species);

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"disease or pathogen" (*e.g.*, fungal, bacterial, and viral causes) ; or "no threat". Note that studies could be classified into more than one of the threat categories.

Question 5: Where were experiments on foundation species done?

We counted the number of studies on foundation species done in each country. We recognize that these data were biased toward journals printed in English and that national or regional resources will influence where foundation species are studied. However, as a first pass of the citation record, identifying geographic location of the studies allowed us to identify regions where the study of foundation species is focused.

Question 6: To what extent did Ellison et al. (2005) influence research on foundation species?

We inferred strength of influence from the results of three of the previous questions. Influence was based on 1) whether the definition of foundation species followed Ellison et al. (2005) (question 1); 2) if the foundation species was identified as the main study organism (question 2); and 3) identification of possible threats to foundation species loss (question 4). Studies that contained all three qualities were categorized as "Strongly Influenced." Studies that contain two qualities in any combination were categorized as "Moderately Influenced." Studies that contain one quality were categorized as "Marginally Influenced."

DATA ANALYSIS

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All data were analyzed using RStudio version 3.0.2 (R Core Team 2013). The packages “maps” (Brownrigg and Minka 2014), “plotrix” (Lemon et al. 2015), and “rworldmap” (South 2013) were used to display geographic locations of surveyed studies. The package “plyr” (Wickham 2014) was used for data frame manipulation. Because our sample size was large and no experiment was conducted (Gotelli and Ellison 2013), we coded the answers to our *Questions* as categorical data and analyzed them using Pearson’s chi-square statistic (Pearson 1900) in the R package “MASS” (Ripley et al. 2013).

RESULTS AND DISCUSSION

Papers citing Ellison et al. (2005) came from 15 countries on 6 continents. Most of the studies were conducted in the United States, while papers on foundation species from mainland Asia were notably absent (Fig. 3). These data suggest that the reach of, interest in, or concern for foundation species applies mainly to the Americas, and that loss of foundation species is not yet a global concern.

Foundation species was not mentioned in every paper and 43% (143) of the studies reviewed did not define the concept (Fig. 2). When it was defined, Ellison et al.’s definition was cited 42% of the time and more frequently than Dayton’s (2%), the combination of Dayton’s and Ellison’s (3%), or other definitions (10%) (Fig. 2). These last 33 papers defined *foundation species* as something other than the original concept or used multiple defining terms, including: *ecosystem engineer* (7), *keystone* (7), *a definer, driver, or supporter of forest structure* (9), *dominant species* (8), *trees* (2), *framework species* (2), *long-lived and widespread* (2), or *foundation genus* (1). Another 16 authors cited for definitions of foundation species include Whitham *et al.* 2006 (2), Grime 1998 (1),

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Whitaker 1965 (1), Gibson et al. 2012 (1), Snyder et al. 2002 (1), Ross et al. 2003 (1), Bruno and Bertness 2001 (1), Homyack et al. 2011 (1), Angelini et al. 2011 (1), Jones 1994 (1), Jones 1997 (2), Heiman and Michli 2010 (1), Kreyling et al. 2011 (1), MacAuther 1984 (1), Paine 1995 (1), and Walker and Chapin 1987 (1). These data suggest that the researchers have not yet converged on a single definition of foundation species and that many researchers may not be aware of the foundation species concept as a concept distinct from other descriptive terms for species that are “important” in ecosystems.

Study organisms were identified as a foundation species in 50% of the reviewed papers that cited Ellison et al. (2005). There was no significant difference in the number of studies that did or did not identify the study organism as a foundation species (Fig. 2). The remaining papers did not specifically identify a study organism as a foundation species (Fig. 2) or only mentioned the concept in passing. These data suggest either that foundation species were not being researched, or that species being studied were not identified as such.

Among studies that did identify foundation species, 34% studied their role in community interactions, 32% studied both community interactions and ecosystem processes, and 22% studied ecosystem processes alone (Fig. 2). The remainder 12% did not identify any specific role of foundation species in the study system (Fig. 2). These data suggest that community ecologists either may be more familiar with or show greater interest in the foundation species concept than ecosystem ecologists.

Eighty-four percent of the studies identified a threat or potential threat to a foundation species (Fig. 2). The most frequently reported threat to foundation species was invasive species (24%), followed by climate change (18%), disease or pathogens (16%), habitat loss or degradation (16%), and exploitation (10%) (Fig. 2). These data suggest that foundation species are being studied during

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or after population loss has already begun. We note that the emphasis on threats to foundation species by nonnative species contrasts with threats identified for rare species. In the latter, the vast majority (81%) were reported to be threatened by habitat loss, whereas only 57% were reported to be threatened by invasive species (Wilcove et al. 1998). These data suggest that research on foundation species has not followed the recommendations to study them before they were threatened. We conclude that Ellison's suggestions to increase study of foundation species and leverage the opportunity to study foundation species during decline have been largely ignored for many (though not all) species, and that research on foundation species is still lagging except in cases where species are threatened (*e.g.*, Prevèy et al. 2010, Garneau et al. 2012, Vose et al. 2013).

Finally, there were nearly 1.5 times more papers in the present dataset that were "Marginally Influenced" by Ellison et al. (2005) than were "Strongly Influenced" (Fig. 2), suggesting that Ellison et al. (2005) was being cited for reasons other than supporting research on foundation species. This may not be unexpected as Ellison et al. (2005) used several case studies to illustrate the importance of foundation species loss including eastern hemlock (*Tsuga canadensis* (L.) Carr.), whitebark pine and America chestnut (*Castanea dentate* (Marsh.) Borkh.). Focus on content related to these species may have been higher than for the overarching message of the paper. Indeed, many of the citations to Ellison et al. (2005) in the first few years after it was published were focused primarily on the case studies contained in the paper and not specifically on the concept of foundation species. In many such cases, the term "foundation species" was never mentioned in the citing paper and the general concept was not discussed (Fig. 2). Alternatively, the citations could have been 1) "ambiguous", "empty", or "not supported" (Todd et al. 2007), 2) that Ellison et al. (2005) was mis-cited or misprint (Simkin and Roychowdhury 2003), or 3) that it was not completely read (Ball 2002, Simkin and Roychowdhury 2003).

It also is possible that, despite a high citation rate, there is little interest in the foundation species concept itself, the concept is not considered useful, or there has been a failure to distinguish "foundation species" from other common species classifications (Fig. 1). The likelihood that the foundation species concept is underrepresented is supported by examination of species excluded from the citation analysis through personal experience of the authors. For example, longleaf pine (*Pinus palustris* Mill.) displays all the critical characteristics of a foundation species and has received considerable attention in the literature (*e.g.*, Van Lear et al. 2005, Kirkman et al. 2013). Like American chestnut, eastern hemlock, and a number of other species in papers covered by our citation analysis, longleaf pine was a dominant species in its original range, was abundant throughout a wide geographic area, and possessed specific characteristics that supported unique communities and controlled ecosystem processes (Van Lear et al. 2005, Butler et al. 2014). Also like American chestnut, the species has mostly disappeared from its historic range (Van Lear et al. 2005, Butler et al. 2014). Yet, this species is completely absent from the citation analysis because researchers who study it have not classified it as a foundation species.

To further advance foundation species research, we suggest an integrated framework that tracks the research cycle from definition and scoping through conservation and management (Fig. 4). We intend this framework to both improve the recognition of foundation species and provide a general workflow for prioritizing research and/or conservation conditional on threats to a particular foundation species. Because one of the more interesting take home messages from this analysis is that foundation species were not identified as such, we encourage researchers to distinguish "foundation species" from other categories of important species so that their research can find a place in this framework and contribute additional and cumulative knowledge of foundation species research (Fig. 1).

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We also think this conceptual diagram will be particularly useful for ecosystem and community ecologists studying species for which threats have yet to be identified (Fig. 4). Ecosystem science tends to focus is on total system fluxes and, by necessity, simplify ecosystems using stand-wide parameters (*e.g.* leaf area index) regardless of individual species characteristics. In such cases, the system is treated as the subject rather that the species, even when system processes may be highly species-dependent. Examples of the unique role that foundation species can have in undisturbed conditions may identify characteristics that make ecosystem either vulnerable or resilient to change.

Lastly, we believe this framework will help land managers discover commonalities between their species of interest and other foundations species. These commonalities might include threats to the ecosystems and/or lessons learned about the effectiveness of specific management techniques applied to a given situation. These could be particularly useful for conservationists who are looking for case-studies of restoration to use as examples for species that are becoming more vulnerable as disturbances increase. For the land manager interested in restoration, these studies can also provide insight into the possible desired future conditions of other ecosystems being considered for restoration. Thus, to fully account for the influence of foundation species, there is a need to communicate the importance of foundation species to the broader scientific community so that important studies on stable systems or systems that have been successfully restored can be included (*e.g*. through keywords, etc.) and further our understanding of the role of foundation species in ecosystem structure, function and resilience.

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We do not suggest that we have identified all potential foundation species through our citation analysis and call on other scientists, especially ecosystem scientists, to consider whether they are studying a foundation species and identify those species as such. Nor do we mean to suggest that scientists are unaware that they are studying important species; on the contrary, having studied foundation species it seems likely that their importance is valued. We hope that in the future foundation species will be universally recognized as such and identified in the literature whenever appropriate so that we can coordinate efforts to understand and conserve them. Such species, and the systems that depend on them, may serve as valuable models of resistant and resilient ecosystems and the lessons learned can be applied to areas experiencing similar change.

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Figure 1. Comparison of characteristics that differentiate commonly used terms that describe common and/or abundant species.

Figure 2. Summary of general trends in the study of foundation species based on the results of the Ellison et al. 2005 study (solid lines represent the pool of studies from one analyzed question to the next; dotted lines indicate side information on how results of questions were broken down of each result; filled circles show direction of significance based on Chi^2 results; p-values from Chi^2).

Figure 3. Geographic map of the number of studies (circle size) that identified research organism as foundation species (FS) (green) and the studies that did not identify foundation species (blue).

Figure 4. Suggested approach to foundation species research and how topics are connected in the scope of this paper. The definition of the foundation species concept is directly related to the correct identification of a foundation species. The correct identification allows researchers to identify the species foundation species role in the ecosystem, which allow for quantification of the foundation species ecosystem services. The interaction between ecosystem services and specific ecosystem roles provides information on how foundation species roles (support species and stabilize microclimate) may influence ecosystem services at different levels. The ability to identify vulnerabilities to foundation species will allow researchers to identify ecosystem change in response to loss. Conservation management strategies could be studied before a threat to a particular foundation species becomes a problem. The increase of foundation species research will help to define and continue stressing the importance of foundations species in ecosystem function (arrows indicate the direction and relationship to topics).

318 **Figure 1.**

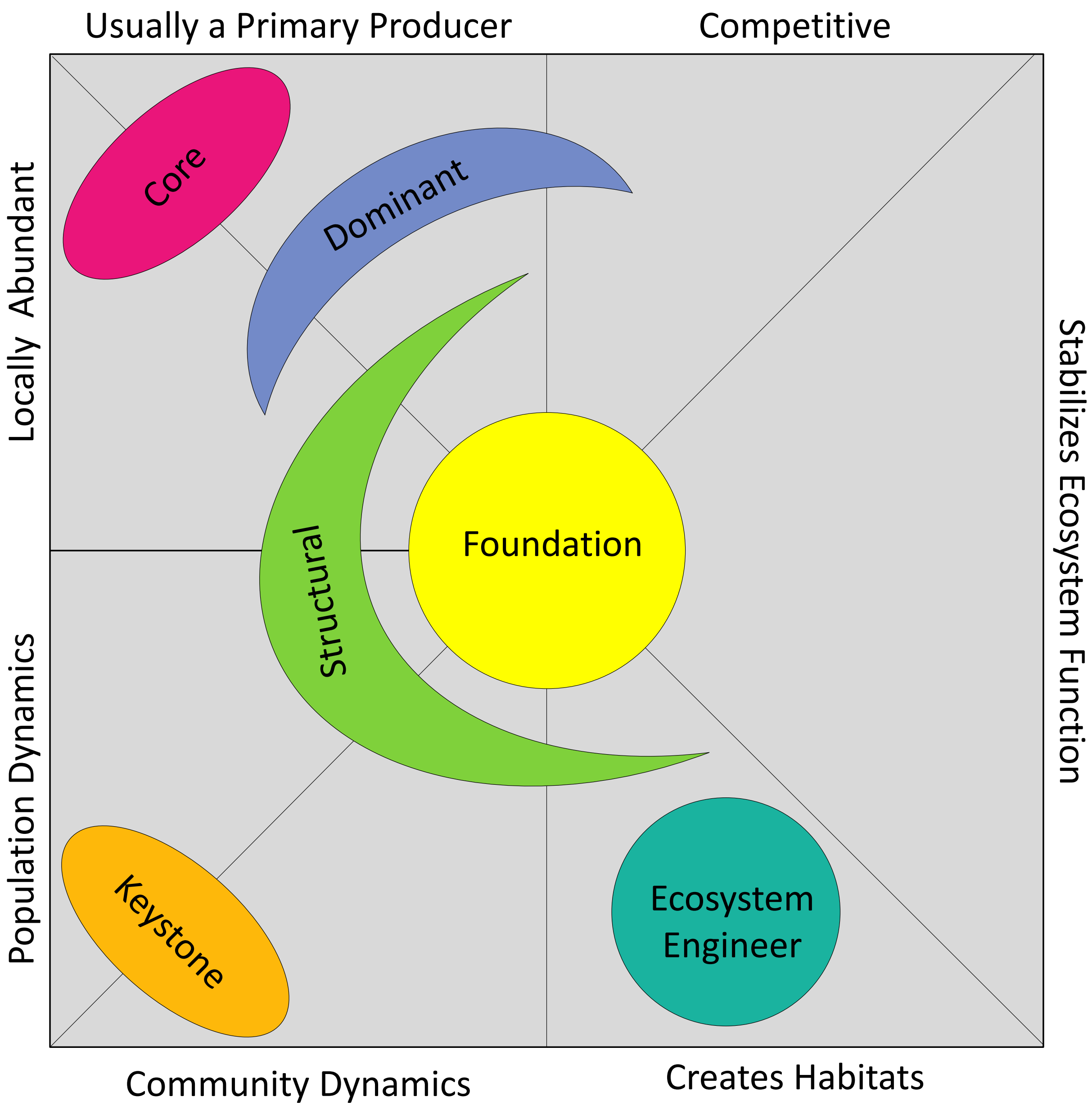

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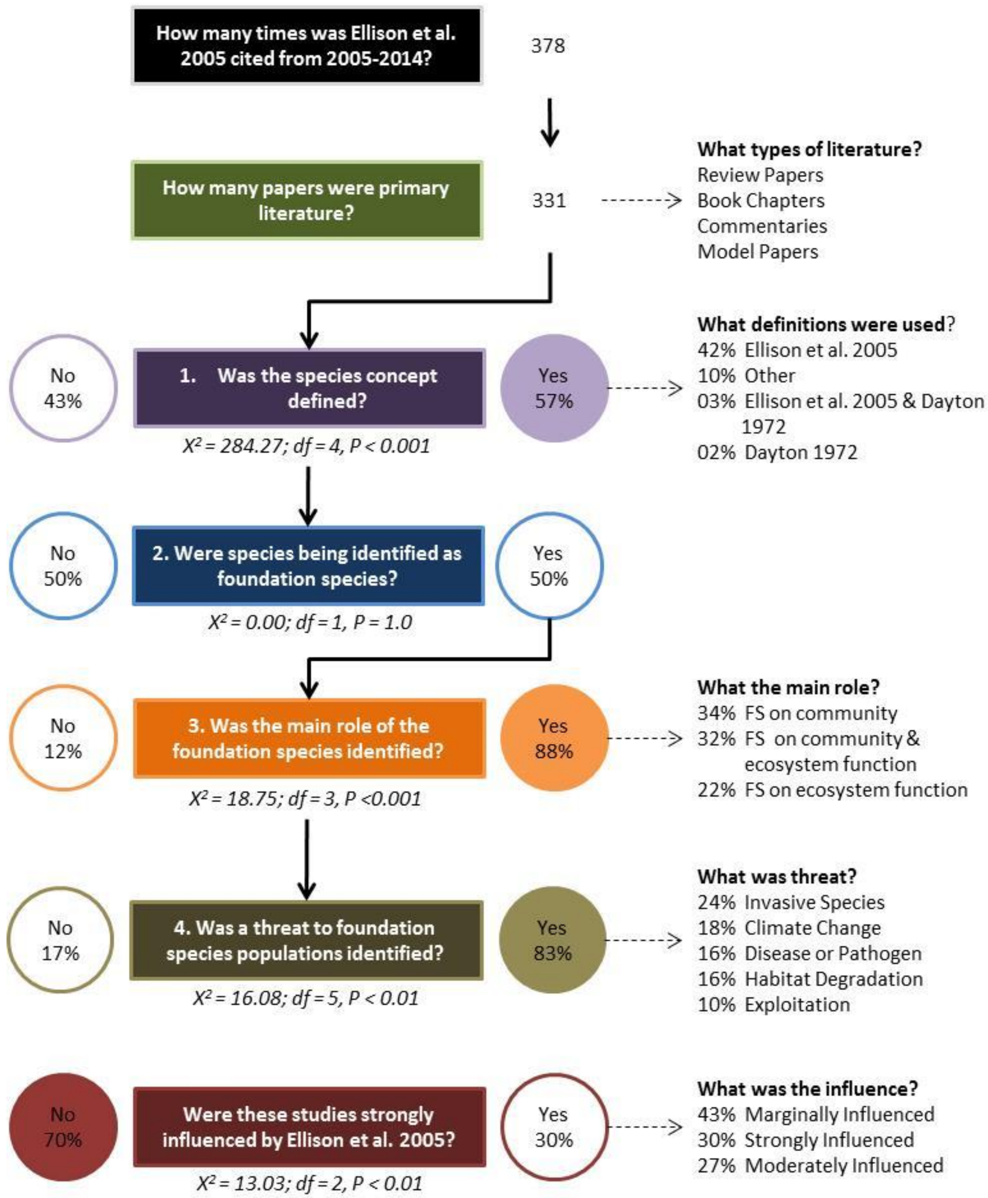
Figure 2.



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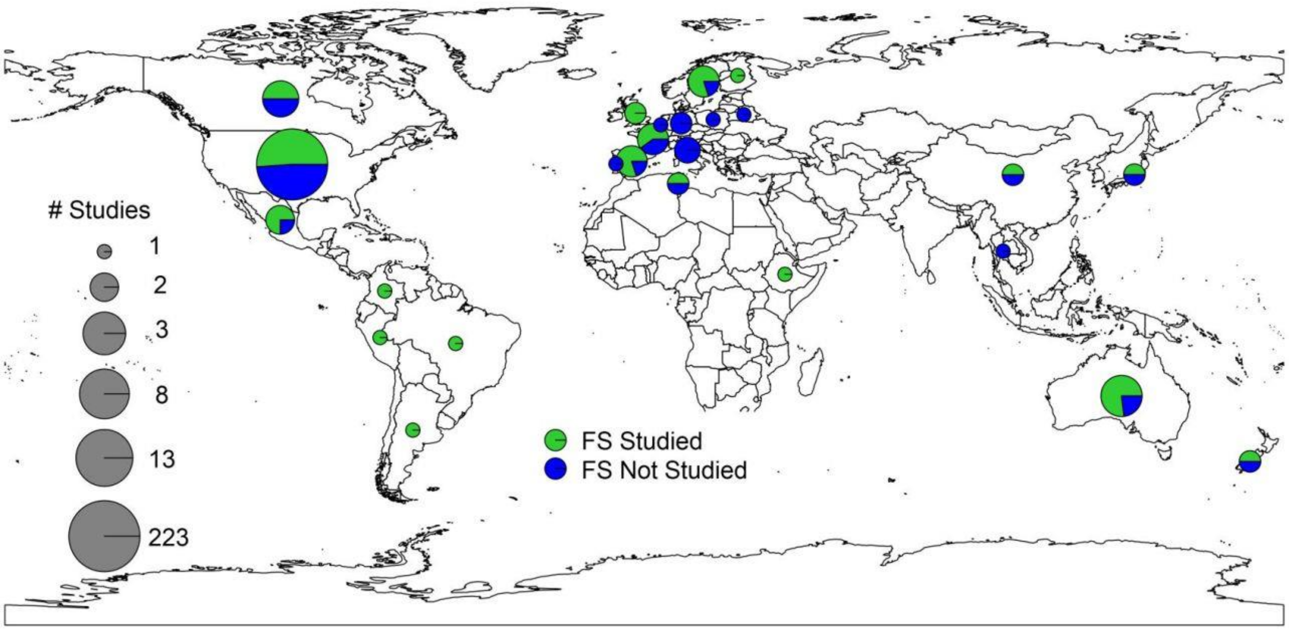
321 **Figure 3.**



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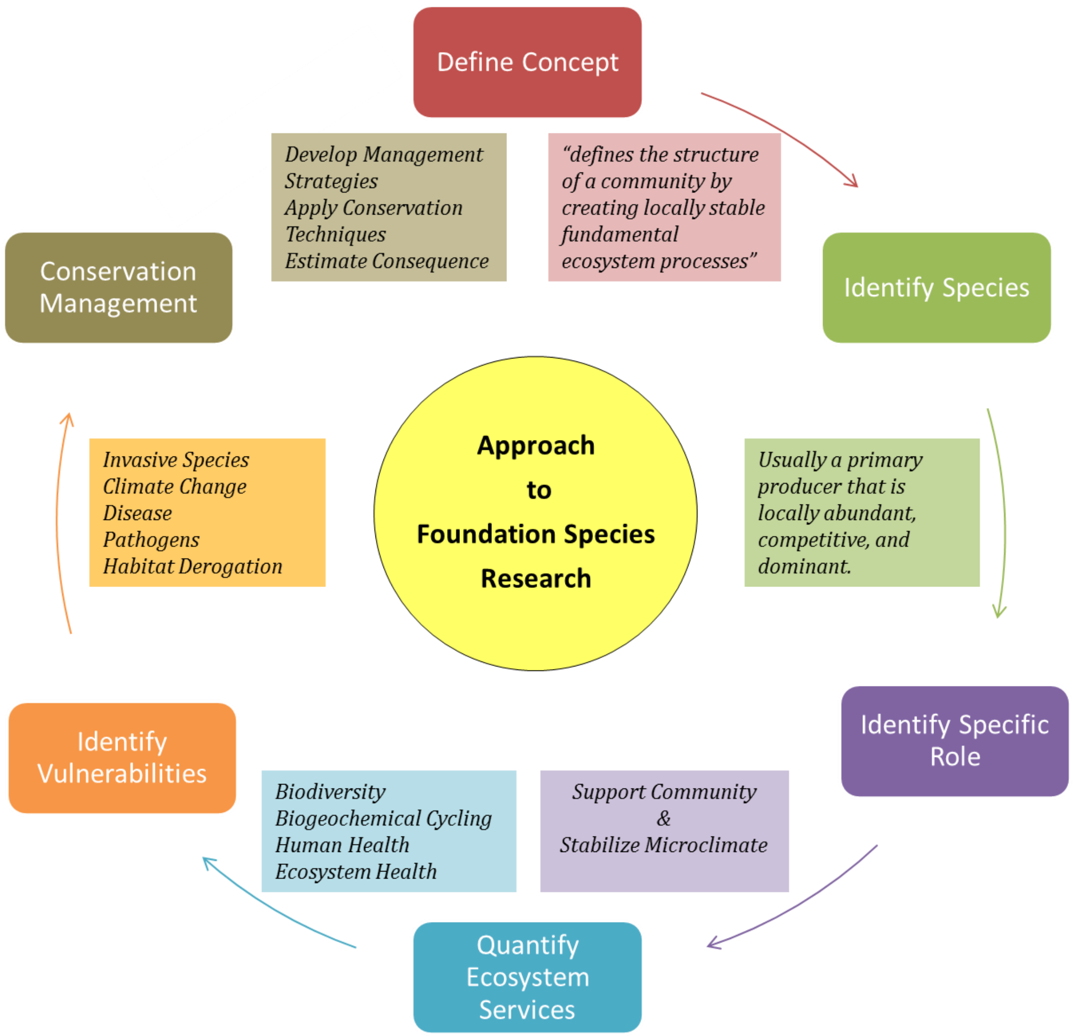
323 **Figure 4.**


Define Concept
"defines the structure of a community by creating locally stable fundamental ecosystem processes"
Identify Species
Usually a primary producer that is locally abundant, competitive, and dominant.
Identify Specific Role
Support Community & Stabilize Microclimate
Quantify Ecosystem Services
Biodiversity
Biogeochemical Cycling
Human Health
Ecosystem Health
Identify Vulnerabilities
Invasive Species
Climate Change
Disease
Pathogens
Habitat Derogation
Conservation Management
Develop Management Strategies
Apply Conservation Techniques
Estimate Consequence
Approach to Foundation Species Research