Rare Species and Ecosystem Functioning

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Abstract: *The role of diversity in the maintenance of ecosystems has been studied widely in the past decade. By correlating richness and diversity with basic ecosystem processes, these investigations lend support to the hypothesis that species diversity significantly influences ecosystem functioning and, in turn, provide support for the conservation of biodiversity. Nonetheless, the majority of these investigations demonstrate that conservation of a relatively small number of generally dominant species is sufficient to maintain most processes. Indeed, there is remarkably little evidence to support the contention that less common species, those likely of highest conservation concern, are important in the maintenance of ecosystem functioning. Here we summarize studies, most employing alternative methodological strategies, wherein less common and rare species are demonstrated to make significant contributions to ecosystem functioning. Evidence exists among studies of keystone species, aggregate effects of less common species, and species turnover. Our findings suggest that (1) less common species can make significant ecosystem contributions; (2) further investigation into the effects of rare and less common species on ecosystem maintenance is sorely needed; (3) further investigation should embrace a variety of approaches; and (4) until further research is conducted a prudent conservation approach is warranted wherein the contribution of less common species to ecosystem functioning is assumed.*

Key Words: keystone species, species diversity, species turnover

Especies Raras y Funcionamiento del Ecosistema

Resumen: *El papel de la diversidad en el mantenimiento de los ecosistemas ha sido ampliamente estudiado en la última década. Al correlacionar riqueza y diversidad con procesos ecosistémicos básicos, estas investigaciones dan sustento a la hipótesis de que la diversidad de especies influye significativamente en el funcionamiento del ecosistema y, a su vez, proporciona soporte para la conservación de biodiversidad. Sin embargo, la mayoría de estas investigaciones demuestran que la conservación de un número relativamente pequeño de especies generalmente dominantes es suficiente para mantener a la mayoría de los procesos. Ciertamente, es notable la escasa evidencia para sustentar el argumento de que las especies menos comunes, probablemente las de mayor preocupación para la conservación, son importantes para el mantenimiento del funcionamiento de los ecosistemas. Aquí resumimos estudios, la mayoría de los cuales emplearon estrategias metodológicas alternativas, que demuestran que las especies menos comunes y raras contribuyen significativamente al funcionamiento del ecosistema. Existe evidencia en estudios de especies clave, de los efectos de especies menos comunes y de recambio de especies. Nuestros hallazgos sugieren que (1) las especies menos comunes pueden hacer contribuciones significativas al ecosistema; (2) se requiere más investigación del efecto de especies menos comunes y raras; (3) la investigación futura debería incluir una variedad de estrategias y*

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Paper submitted November 18, 2003; revised manuscript accepted October 21, 2004.

Conservation Biology 1019–1024

DOI: 10.1111/j.1523-1739.2005.00106.x

(4) en tanto haya más investigación se justifica una estrategia conservadora que da por hecho la contribución de las especies menos comunes al funcionamiento del ecosistema.

Palabras Clave: diversidad de especies, especies clave, recambio de especies

Introduction

Studies of the role of diversity in the maintenance of ecosystem stability are among the oldest in the history of modern ecology (Hector & Hooper 2002). In the last decade focus on the subject has intensified and has evolved into investigations of the role of diversity in maintaining ecosystem functioning and services, and an enormous body of research testing these relationships now exists (e.g., Frank & McNaughton 1991; Naeem et al. 1995; McGrady-Steed et al. 1997; Symstad et al. 1998; Hector et al. 1999; Tilman et al. 2001). This research has given rise to an inordinately large number of essays (e.g., Hector et al. 2001; Loreau et al. 2001; Zedler et al. 2001), reviews (e.g., Goodman 1975; Naeem et al. 1994; Chapin et al. 2000), and books (e.g., Daily 1997; Kinzig et al. 2001; Wardle 2002) on the subject.

Based on simple correlations between diversity and measures of ecosystem functioning, consensus is growing for the argument that biodiversity must be conserved to maintain ecosystems. Schwartz et al. (2000) challenged this widespread conclusion in a review of empirical studies demonstrating that, in most cases, the relationship between diversity and ecosystem processes was not linear but asymptotic. In contrast to the prevailing interpretation, an asymptotic relationship suggests that ecosystem functioning may be maintained by conservation of relatively few, generally dominant species, not the whole of diversity.

In the majority of ecological communities most species exist in relatively low abundance (Rabinowitz et al. 1986; Howe 1999) and, as such, are expected to be at higher risk of extinction (e.g., Purvis et al. 2000). Nonetheless, because of logistical, intellectual, and financial constraints, studies on biodiversity and ecosystem functioning focus primarily on common species. In addition, it seems logical to assume that species with low abundances will have concomitantly low ecosystem impacts, as argued by Grime (1998) in his mass ratio theory. Consequently, the literature addressing the contribution of diversity to ecosystem functioning is chiefly limited to those species likely to make large ecosystem impacts because of their high relative abundance (Schwartz et al. 2000; Lawler et al. 2001). The result is a lack of information to make the general conclusion that the maintenance of an entire suite of community species is necessary to maintain ecosystem functioning.

Schwartz et al. (2000), and later Hector et al. (2001), argue that a lack of information regarding at-risk species requires that we rely on a precautionary approach, albeit scientifically unsatisfying. This is not a new concept. Leopold (1953) and Ehrlich and Mooney (1983) similarly advocate that, in lieu of evidence to the contrary, all species be assumed to contribute in important ways to the ecosystems in which they exist. This approach is justifiable, however, only if we find that less common or rare species can contribute significantly to ecosystem functioning. Given that we rarely study the specific effects of uncommon species on ecosystem properties, we know little about the role these species may play in ecosystems. If, on occasion, we demonstrate that less common species do have strong impacts on ecosystem stability and functioning, a precautionary approach is warranted because of the possibility that many other not-yet-studied species may be important.

To substantiate the precautionary approach we located case studies providing evidence that less abundant species in a community, those often overlooked in conventional studies of the relationship between diversity and ecosystem functioning, make significant, measurable contributions to their ecosystems. We did not aim to quantify how often less common species are demonstrated to contribute to valued ecosystem attributes. We propose that a precautionary approach is warranted if we find that less common species, in those rare cases where they are the focus of a study, are demonstrated to make substantial contributions to ecosystem functioning. We grouped the studies into three categories: (1) less common species as keystone species, (2) effects of less common species when considered in aggregate, and (3) spatial and temporal turnover of less common species.

Many measures have been used to examine the role of species in ecosystems. Among these metrics are measures of ecosystem processes and ecosystem services. Ecosystem processes are frequently used as a measure because they are assumed to be related in some way to ecosystem health or ecosystem functioning. The most commonly measured ecosystem processes include biomass production and nutrient cycling (typically measured by looking at metrics such as nitrogen retention or movement of carbon between different carbon pools). In general, ecosystem processes involve the movement of materials and energy through an ecosystem and include processes such as nutrient retention and cycling, water retention, productivity, community respiration, and stability. When the ecosystem process in question has a direct effect on human health or economic well-being, it is also called an ecosystem service (Daily 1997; Naeem 1998). Common ecosystem services include water filtration, oxygen production, timber production, and erosion control.

Rarity has several forms (sensu Rabinowitz et al. 1986). For the purpose of this discussion, we focused on studies in which the authors suggest or explicitly define a species as less common, rare, or subdominant. We were primarily concerned with species that represent a small component of ecosystem biomass (~1–5%) within their trophic level and nonetheless demonstrate strong effects on ecosystem attributes.

Less Common Species as Keystone Species

Among studies of keystone species we expected to find many examples where relatively less common species had large ecosystem impacts because keystone species are defined as species with functional impacts disproportional to their abundance. In their review of keystone species, Power et al. (1996) provide numerous examples of taxa found at relatively low abundance in their communities with major impacts (e.g., beaver [*Castor canadensis*], bass [*Micropterus* spp.], gophers [*Geomys bursarius, Thomomys bottae*], and snow geese [*Chen caerulescens*]). Most species were too common for us to include here; we found appropriate examples among top predators, however, which tend to contribute relatively little to overall ecosystem biomass.

The loss of top predators can degrade ecosystems (e.g., Ceballos & Brown 1995; Purvis et al. 2000; Duffy 2003). One example of costs associated with removal of top predators is the frequent population explosions of white-tailed deer (*Odocoileus virginianus*) in the eastern United States during the past 50 years (McShea et al. 1997). Natural control through the actions of native predators is a function that has been lost in many ecosystems. An overabundance of deer causes loss of plant diversity and eventual habitat degradation through overbrowsing of preferred species (e.g., Anderson 1997; Seagle & Liang 1997; Stromayer & Warren 1997; Brooks 1999; Webster & Parker 2000; Anderson et al. 2001). Large deer populations also increase the spread of Lyme disease in humans (VanBuskirk & Ostfeld 1995; Jones et al. 1998) and human fatalities through nighttime automobile-deer collisions (Groot-Bruinderink & Hazebroek 1996; McCullough et al. 1997). In this case, the loss of uncommon species (top predators) has resulted in a decline in ecosystem services.

Uncommon plant species can act as keystone species in soil resource dynamics. For example, a suite of *Equisetum* species in a cold-temperate Alaskan shrub wetland, constituting <5% of the above- and belowground biomass, make substantial contributions to ecosystem processes (Marsh et al. 2000). Despite their relatively low representation as a portion of the total community phytomass, *Equisetum* spp. contribute 29% P and 39% K to the total annual litter accumulation and 55% P, 41% K, and 75% Ca to 2-year-old soil nutrient pools. The roots of *Equisetum* spp. occupy the lower C soil horizons in this marsh system, and roots of the remaining species occupy the upper O horizons. Marsh et al. (2000) suggest that *Equisetum* spp. act as nutrient pumps that move limiting resources such as P, and to a lesser extent K and C, from lower to higher soil horizons, making them available to plant community dominants such as *Myrica gale*, *Salix* spp., and *Carex* spp. The sequestration of copious amounts of nutrients in these relatively unpalatable species, which contain high tissue concentrations of silica and thiaminase, may also be important in the maintenance of nutrients in this system, which is highly affected by the grazing of moose and hare. Furthermore, although decomposition rates in this anaerobic and cold environment are slow, *Equisetum* spp. are relatively quickly mineralized and contribute to higher rates of nutrient cycling. The findings of Marsh et al. (2000) may also explain the high concentrations of phosphorus in ponds dominated by *Equisetum* spp., suggesting that the ecosystem contributions of these uncommon species may be further reaching.

Aggregate Effects of Diversity

Ecologists have also documented the role of diversity in ecosystem functioning by aggregating the effects of less common species on the system as a whole. As is common among abundant taxa in a community, there may be key players among rare species for a given ecosystem process and an efficient method to detect these species is to treat them in aggregate.

Less common species can be important in the resistance of a community to new species invasions. Lyons and Schwartz (2001) reduced plant community diversity by removing the less dominant species. Once diversity was significantly lower than the controls, they introduced an exotic grass. The diversity-reduction treatment experienced significantly higher rates of colonization than the control treatments. In addition, there was a significant positive correlation between the number of less common species removed and colonization of the introduced species. The results of this study suggest that invasion resistance may be conveyed by the aggregate effect of less common species on available resources. More important, a linear relationship between richness and colonization demonstrates that species removal results in incremental loss of ecosystem resistance to colonization, emphasizing the role of each species as a factor in the process.

Less common species in aggregate also can play an important role in nutrient cycling and retention (Theodose et al. 1996). In an alpine meadow differences were found between early- and late-season nitrogen uptake rates among rare, subdominant, and dominant species. It was hypothesized that dominant species were outcompeting less common species in this high-stress environment by usurping vital and limiting resources such as nitrogen. To determine seasonal uptake rates, a liquid solution of radioactively labeled nitrogen (^{15}N) was added at the beginning and middle of the growing season. Surprisingly, the highest per capita N concentrations were consistently found in rare and subdominant species, whereas dominant species had higher N-use efficiencies. Thus, elimination of less abundant taxa from this ecosystem could result in diminished retention of limited nutrients.

Temporal Variability in Species Abundance

At any single time, the majority of species within an ecosystem are uncommon. Nonetheless, these uncommon species may play critical roles in the ecosystem by becoming dominant following particular environmental triggers. Thus, one way a species typically perceived as less common may play an important role in ecosystem functioning is through changes in its abundance over time. It is therefore critical to understand the potential impacts of fluctuations in abundance on ecosystem functioning.

Variability in species abundance has been well documented in studies of succession (Vankat 1991; Gibson et al. 1992; Hollier & Belshaw 1992; Myster & Pickett 1992; Robinson et al. 1992; Root & Cappuccino 1992); response to disturbance such as fire, flooding, and hurricanes (Heikens et al. 1994; Parmenter et al. 1997; Cooper-Ellis et al. 1999; Courtemanche et al. 1999; Sanchez & Islebe 1999; Lugo et al. 2000; Platt et al. 2000; Boose et al. 2001); and response to change in environmental conditions such as rainfall (Huntly & Chesson 1994; Huntly et al. 1996). Although these shifts in abundance have been studied with respect to their role in maintenance of diversity and species coexistence (e.g., Chesson 1986; Chesson 1994; Tilman 1994), they have yet to be examined with respect to the role that less common species play in maintaining ecosystem functioning.

Many less common plant species have been characterized as dependent on openings created by fire for persistence (Quintana-Ascencio & Menges 2000). Such plants often respond to fire by occupying recently burned sites before recolonization by superior competitors. For instance, three narrowly endemic species have seedbanks that germinate following fire (Quintana-Ascencio & Menges 2000). This response is common in chaparral (e.g., Keeley 1996; Keeley & Fotheringham 1998*a*,*b*). All three narrowly endemic species have higher survival, larger biomass, and greater fecundity in recently burned areas (Quintana-Ascencio & Menges 2000). The species are generally found only in recently burned openings, and their abundance declines as the time since fire increases (Menges & Kimmich 1996). Postfire, early germinating and otherwise uncommon plant species may stabilize soils and maintain vegetative cover until more common species recolonize.

Walker et al. (1999) hypothesize that functionally similar minor and dominant species provide buffering against environmental perturbations such as increased herbivory. Specifically, minor species, functionally similar to dominant species but with different environmental requirements and tolerances, may increase resilience in ecosystem functioning under perturbations that favor them over the past dominants. Walker et al. (1999) tested this theory in a lightly grazed versus heavily grazed site and found that species of low abundance in a lightly grazed site compensated for the functions provided by dominants in a more heavily grazed site. The findings of Walker et al. (1999) are supported by theoretical work of Yachi and Loreau (1999), who demonstrate that the replacement of dominants by previously rare species buffers and enhances ecosystem processes in the face of environmental stochasticity.

Although the tendency of insect populations to vary in size over time is well documented (e.g., Huntly 1991), the ecological literature on the potential role of outbreaks of insect herbivores on ecosystems is scarce. Carson and Root (2000) document six cases from the literature where outbreaks had large effects on vegetation. These cases include grasshoppers in prairies (Capinera 1987), spruce budworm (*Choristoneura fumiferana*) (Cappuccino et al. 1998), and ghost moths (*Hepialus humuli*) (Maron & Connors 1996) and suggest that the role of insect outbreaks in suppressing dominants may be much more common than was previously thought. During outbreak events herbivores cause long-term damage to hosts and increase light levels in the understory. These effects provide opportunities for growth and establishment of species in the understory and increasing tree seedling establishment. Thus, insects that are typically at low abundance within a system can have large ecosystem effects when their abundance increases during outbreaks.

Similarly, a study of pollination service in row crops by native bees demonstrates that the aggregate contribution of less common species is essential in sustaining a system with high yearly variation in species composition and abundance (Kremen et al. 2002). In one year of the study, during which many species were low in abundance, the aggregate contribution of all species was required in order to reach a threshold necessary for sufficient crop pollination. Because of higher abundances in the second year, only a few species were required to reach the threshold. Temporal variability in species abundances was important in the maintenance of pollination service because in each year several of the most important contributors were either minor or entirely absent in the other year.

Conclusions

To assert that the whole of biological diversity should be conserved to maintain ecosystem properties, one must be able to demonstrate that less common species also make significant contributions. This is a challenging task within the current context of investigations into the role of biodiversity in ecosystem functioning because understandable logistical constraints to experimental research in this area limit our ability to explore the range and breadth of potential ways less common species contribute to ecosystem values.

Indeed, with few exceptions (e.g., Lyons & Schwartz 2001), the studies reported on here fall outside the conventional approach in which experiments are designed to seek a strict correlation between diversity and ecosystem processes (for further discussion see Schwartz et al. 2000). Also noteworthy and of particular concern to the conventional approach is evidence that abundance can be an unreliable measure of impact (e.g., Walker et al. 1999). In our literature search we found a limited number of studies explicitly addressing the role of rare and less common species in ecosystem maintenance. Nonetheless, among these studies the evidence is compelling. Not surprisingly, we found no studies reporting negative results.

At this time, biotic and abiotic interactions of a majority of the species on the planet are unknown or poorly understood. Our survey suggests this is doubly true for rare and less common species. In the short term, widespread ignorance warrants a precautionary approach regarding taxa with putatively less ecosystem impact. Effective and compelling arguments for the future preservation of the whole of biological diversity will require more information on the ecosystem contributions of less common species.

Acknowledgments

We thank SPICE Laboratory members J. Hoeksema and P. VanMantgem for inspiration and C. Kremen, G. Meffe, S. Lawlor, M. Loreau, and anonymous reviewers for their thoughtful contributions.

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