CONCEPTS & SYNTHESIS

EMPHASIZING NEW IDEAS TO STIMULATE RESEARCH IN ECOLOGY

PREDICTING EFFECTS OF ECOSYSTEM ENGINEERS ON PATCH-SCALE SPECIES RICHNESS FROM PRIMARY PRODUCTIVITY

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Abstract. Ecosystem engineering—the physical modification of habitats by organisms—can create patches with altered species richness relative to adjacent, unmodified patches. The effect of ecosystem engineering on patch-scale species richness is likely to be difficult to predict from the identity of the engineer, the resources altered as a result of engineering, or the identities of the affected species. Here we develop a simple conceptual model that predicts the effects of ecosystem engineers on species richness based on how the habitat modifications caused by engineers affect primary productivity, assuming a hump-shaped relationship between productivity and species richness. We review data from 35 studies that contained 60 comparisons of species richness on patches that had been modified by ecosystem engineers vs. unmodified patches. We found no general patterns in whether species richness at the patch scale was increased or decreased by ecosystem engineering. However, 14 of these studies also contained data on primary productivity on and off engineered patches, giving 30 cases to: (1) test whether the effects of ecosystem engineering on richness depend upon the productivity of the ecosystem, and (2) examine the effect of the engineer on productivity. Matching the predictions of the conceptual model, we found a significant negative relationship between productivity and the engineering effect on species richness when ecosystem engineers increased productivity and a weak positive relationship when engineers decreased productivity. We compare the conceptual model developed here to models predicting the effects of grazing and facilitation on species richness. These results, if supported by further studies, can contribute to our general understanding of ecosystem engineering and have important implications regarding the consequences of the loss or introduction of ecosystem engineers on species richness and ecosystem function across landscapes that vary in productivity.

Key words: ecosystem engineering; primary productivity; spatial scale; species richness.

INTRODUCTION

A central goal of community ecology is to understand mechanisms underlying patterns of species richness and community composition. Studies of the effects of individual species on communities have typically focused on predation and competitive interactions. However, organisms can have profound effects via other mechanisms, such as ecosystem engineering—the modification, maintenance, creation, or destruction of habitats (Jones et al. 1994, 1997). In some cases, habitat

modifications by ecosystem engineers are so minor that the effects of ecosystem engineering on species richness or composition are likely trivial. However, given that ecosystem engineering results in patches in which the availability of resources differs from the surrounding habitat that remains unmodified by the engineer, and that the distribution of species tends to be affected by the availability of resources, ecosystem engineering clearly has the potential to affect the distribution and abundance of species (Jones et al. 1997, Crooks 2002, Wright et al. 2002).

Ecosystem engineering comprises diverse activities performed by a diversity of organisms (Jones et al. 1994, 1997, Crooks 2002). Engineers can modify the availability of such resources as water (Yair and Shachak 1982, Dawson 1993), light, nutrients (Jones and Shachak 1990), salinity (Bertness and Hacker 1994), nesting sites (Nummi and Poysa 1997), and solid sub-

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strates for attachment (Crooks and Khim 1999). Some ecosystem engineers, such as beaver, have large and obvious impacts on ecosystems (Naiman et al. 1988) whereas others cause changes of a much smaller magnitude. Ecosystem engineers have been documented in a wide array of terrestrial and aquatic ecosystems, and the same engineering species can modify the environment in similar ways in different ecosystems. Given this diversity, is it possible to predict the effects of ecosystem engineering on species richness? Or is the concept of organisms as ecosystem engineers not useful in trying to understand patterns of species richness because engineering is too idiosyncratic?

Predicting the effect of ecosystem engineering on species richness across scales

The degree to which it is possible to predict the effect of ecosystem engineering on species richness likely depends on the spatial scale of interest. Jones et al. (1997) argued that the effect of ecosystem engineering on species richness at a scale that includes both engineered patches and patches unmodified by that particular ecosystem engineer—the landscape scale— would almost inevitably be positive due to an increase in habitat diversity. Several studies have suggested that ecosystem engineers increase landscape-scale species richness by creating new habitats and allowing species that would otherwise be excluded to persist (Collins and Uno 1983, Inouye et al. 1987, Guo 1996, Ceballos et al. 1999). For example, Wright et al. (2002) estimated that by creating wetlands, beaver increase the number of herbaceous plant species in riparian zones by 33%.

Ecosystem engineering also is likely to have an effect on species richness at smaller scales, particularly when comparing engineered patches with patches unmodified by the engineer—the patch scale. Examples abound in the literature of studies that have compared the species richness of engineered patches to that of patches not modified by the engineer (hereafter termed "unmodified"). Jones et al. (1997) proposed that there was no a priori reason to expect that engineered patches should contain more or less species than unmodified patches. They noted that the answer would depend, among other factors, on the magnitude and nature of the changes in resource availability and the number of species in the regional species pool dependent on the resources. Previous research in a wide range of natural ecosystems generally supports this hypothesis. Engineered patches can have the same (Platt 1975, Wright 2002), higher, (Martinsen et al. 1990, Crooks and Khim 1999), or lower (Bratton 1975, Collins and Uno 1983) species richness than unmodified patches. To date there has been little attempt to synthesize the results from these studies in order to determine if the effects of engineering on species richness at the patch scale is at all predictable.

In principle, if one knew how an ecosystem engineer modified the resources in an engineered patch relative to unmodified patches and how all of the species in the regional species pool respond to such modifications, it would be possible to predict the effect of the engineer on species richness at the patch scale. In practice, few ecosystems are studied well enough to provide such data. What is needed is an approach that combines an understanding of how ecosystem engineers modify the physical environment with general ecological principles that have been shown to apply across ecosystems. Crooks (2002), in a review of the effects of invasive ecosystem engineers, suggested that engineers that increase "habitat complexity" tended to increase either the diversity or abundance of organisms, while engineers that decreased habitat complexity had a negative effect on diversity or abundance. The diversity and abundance measures discussed in his review contain a mix of landscape-scale and patch-scale comparisons of the effects of ecosystem engineers on species richness. However, the results suggested that an approach that uses general ecological principles to develop specific predictions about the effects of ecosystem engineering on species richness at the patch scale has potential value.

Conceptual model

The challenge in predicting the effects of an ecosystem engineer on patch-scale richness is that ecosystem engineers vary in the resources they modify, the ecosystems in which they are active, and the species that they affect. Developing general rules about ecosystem engineering requires looking at a common variable that integrates a diverse assemblage of underlying specific mechanisms that are likely to be correlated with species richness across ecosystems. One such variable is the primary productivity of the ecosystem. Since ecosystem engineering involves changes in the availability of resources, it follows that the primary productivity of an engineered patch is likely to differ from that of an unmodified patch, particularly when the altered resource limits plant growth. Ecosystem engineering has the potential to increase the availability of a limiting resource, thereby increasing productivity, e.g., porcupine diggings in the Negev desert that trap water (Alkon 1999). Alternatively, ecosystem engineering can decrease the availability of resources or increase stress, resulting in lower productivity, e.g., seabird guano deposits that increase ammonia levels to near-toxic concentrations (Gilham 1960).

Productivity has been shown to be correlated with plant species richness at small scales in many ecosystems (reviewed in Grace [1999]), and this relationship is predicted by numerous theories (Grime 1979, Huston 1979, Tilman 1982). Although not universally supported (Waide et al. 1999, Chase and Leibold 2002), there is considerable empirical evidence for a general "hump-shaped" relationship between species richness

and productivity, with low richness at high and low productivity and high richness at intermediate productivity, particularly at smaller spatial scales (Grace 1999, Mittelbach et al. 2001). The most common explanation for this pattern, first articulated by Grime (1979), is that at low productivity, species richness is limited by either stress or disturbance, while at high productivity, patches tend to be dominated by one or a few competitively superior species. At intermediate levels of productivity, rates of competitive displacement are low enough to prevent dominance while resource levels are high enough to support the full assemblage of plants, resulting in higher species richness.

The "hump-shaped" model of the relationship between species richness and productivity suggests that the effect of an ecosystem engineer that creates patches of higher or lower productivity could have systematically varying effects on richness, depending on where along a productivity gradient an ecosystem is situated. An ecosystem engineer that increases productivity in a low-productivity system should have a positive effect on species richness by ameliorating stressful conditions, while one that increases productivity in a highly productive system should further enhance competitive dominance, reducing species richness (Fig. 1A). On the other hand, an ecosystem engineer that creates patches with lower productivity is likely to increase species richness in a high-productivity environment and reduce species richness in a low-productivity environment (Fig. 1B). This model therefore predicts a negative relationship between the productivity of an ecosystem and the effect of an ecosystem engineer on species richness when the engineered patch has higher productivity than the unmodified patch, and a positive relationship when the engineered patch is less productive. Furthermore, the model makes several qualitative predictions about the relationship between ecosystem engineers and species richness at the patch scale. First it suggests that organisms that create patches that have similar effects on primary productivity are likely to have similar effects on species richness regardless of differences in taxonomy or trophic position of the engineers. Second, the same engineer species can have very different effects on species richness if it operates in different ecosystems with different productivities, even though it is modifying the environment in the same manner.

To test both the qualitative and quantitative predictions of the conceptual model, we present a review of the available literature on the effects of ecosystem engineering on species richness and productivity at the patch scale. While the conceptual model may extend to predicting the species richness of animals and microbes, it was developed specifically for plant communities, and thus the review only covers studies of the effects of ecosystem engineers on terrestrial plant species richness. We first review cases that measure species richness on engineered patches and on equiv-
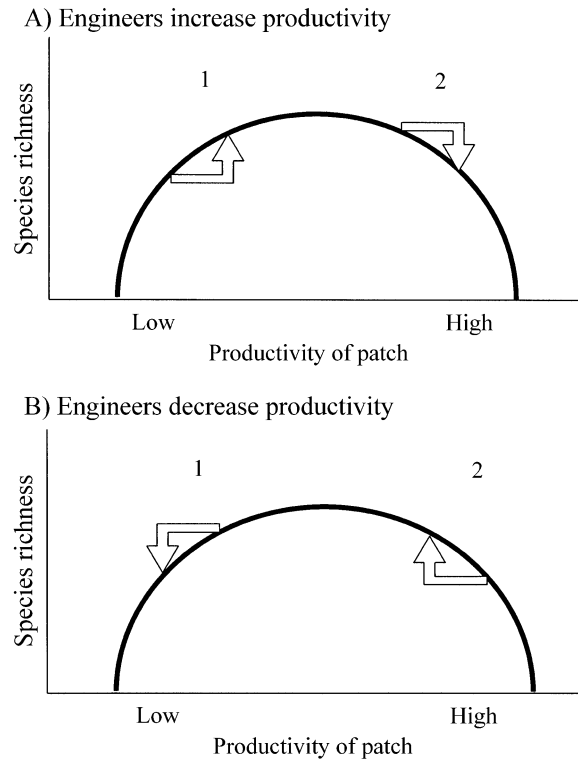

FIG. 1. Conceptual model illustrating how the effects of ecosystem engineering on species richness at the patch scale vary depending on the productivity of the system and whether the ecosystem engineer creates patches with (A) higher and (B) lower productivity than unmodified patches. Species richness in unmodified patches (solid lines) is assumed to show a "hump-shaped" relationship with productivity. Ecosystem engineers that increase productivity in modified patches (panel A) are predicted to create patches with higher species richness than unmodified patches in low-productivity environments (Case 1) and lower species richness in high-productivity environments (Case 2). Ecosystem engineers that decrease productivity (panel B) are predicted to decrease richness in low-productivity environments (Case 1) and increase richness in high-productivity environments (Case 2).

alently sized areas of unmodified habitat within the same ecosystem to determine if there are any general patterns. We then explicitly test the quantitative predictions of the conceptual model by evaluating studies that contain measures of both species richness and productivity both on and off engineered patches.

METHODS

Although the term "ecosystem engineer" first appeared in 1994 (Jones et al. 1994), studies examining the effects of environment-modifying organisms on species richness have a much longer history in ecology. In order to provide as comprehensive a review of such studies as possible, we searched BIOSIS and the ISI Web of Science for articles in English with "species richness" or "species diversity" and "ecosystem engineer," "habitat modification," or "disturbance" in the title, keywords, or abstracts. We also searched for

TABLE 1. Description of literature data showing the effects of ecosystem engineers on species richness at the patch scale, with examples grouped by direction of the engineering effect on richness.

Organism	Structure created	Richness, S		Quadrat size†	Ecosystem	Reference
		On engineered patch	On unmodified patch			
A) Studies in which engineer increased species richness						
Wild boar	grubbing	14.8	13	36 m²	Appalachian forests, early spring	Bratton (1974)
Badger	pit	15.3	12.0	0.2 m²	tall-grass prairie, grazed	Platt (1975)‡
Prairie dog	town	39	34	4 m²	mixed-grass prairie, old town	Coppock et al. (1983)‡
Prairie dog	town	45	34	4 m²	mixed-grass prairie, young town	Coppock et al. (1983)‡
Vole	tunnel	15.1	10.1	0.1 m²	Alaskan tundra	Fox (1985)‡
Pocket gopher	mound	10.2	8.9	0.5 m²	old field (Minnesota, USA)	Inouye et al. (1987)
Porcupine	pit	3	1.3	0.1 m²	Negev desert	Gutterman et al. (1990)‡
Gopher tortoise	mound	2.1	1.5	1 m²	Florida (USA) sandhill forest	Kaczor and Hartnett (1990)
Ant	mound	7.8	5.0	n.a.	*Paspalum vaginautm* grassland, spring	Lewis et al. (1991)
Ant	mound	7.3	4.5	n.a.	*Paspalum vaginatum* grassland, autumn	Lewis et al. (1991)
Ant	mound	8.9	5.7	n.a.	*Scripus californicus* wetland, spring	Lewis et al. (1991)
Ant	mound	10.0	7.4	n.a.	*Scripus californicus* wetland, autumn	Lewis et al. (1991)
Ant	mound	15.3	11.9	n.a.	*Spartina agrentinensis* grassland, spring	Lewis et al. (1991)
Ant	mound	14.2	11.3	n.a.	*Spartina agrentinensis* savanna, spring	Lewis et al. (1991)
Ant	mound	19.2	17.8	n.a.	*Elyonurus muticus* savanna, autumn	Lewis et al. (1991)
Porcupine	pit	3.3–6.7	1.6–4.1	267 cm²	Negev Desert	Boeken et al. (1995)‡
Wild boar	grubbing	16.62	12.57	0.25 m²	California (USA) coastal grassland, 2 yr post grubbing	Kotanen (1995)
Kangaroo rats	mound	4.6	2.6	0.25 m²	Chihuahuan Desert, active mounds, winter	Guo (1996)‡
Kangaroo rats	mound	2.6	1.8	0.25 m²	Chihuahuan Desert, active mounds, summer	Guo (1996)‡
Kangaroo rats	mound	1.6	1.4	0.25 m²	Chihuahuan desert, inactive mounds, summer	Guo (1996)‡
Various mammals	trails	2.9	1.7	1 m²	*Typha* marsh, June	Hewitt and Miyanishi (1997)
Various mammals	trails	3.5	1.8	1 m²	*Typha* marsh, August	Hewitt and Miyanishi (1997)
Vole	burrow	6.3	3.6	1 m²	old field (Germany)	Milton et al. (1997)
Wild boar	grubbing	16.3	10.8	0.3 m²	old field (Germany)	Milton et al. (1997)
Human	pit	4.4–6.9	1.3–3.3	0.018 m²	Negev Desert	Boeken et al. (1998)‡
Berberis buxifolia (shrub)	mound	1.4	0.7	0.5 m²	Patagonian shrubland	Raffaele and Veblen (1998)
Schinus patagonicus (shrub)	mound	3.14	0.3	0.5 m²	Patagonian shrubland	Raffaele and Veblen (1998)
Ant	mound	12.9	4.4	0.04 m²	Negev Desert	Wilby et al. (2001)‡
B) Studies in which engineer decreased species richness						
Heron	guano mound	2.4	5.4	0.25 m²	forest (Michigan, USA)	Weseloh and Brown (1971)
Wild boar	grubbing	16.6	20.3	36 m²	Appalachian forests, late spring	Bratton (1974)
Wild boar	grubbing	17	20.2	36 m²	Appalachian forests, summer	Bratton (1974)
Wild boar	grubbing	4.9	6.1	1 m²	Appalachian forest	Bratton (1975)
Ant	mound	21	25	2 m²	pasture (England)	King (1977)
Ant	mound	40	45	2 m²	pasture (England)	King (1977)
Bison	wallow	6.2	14.2	0.1 m²	grassland, unburned	Collins and Uno (1983)

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TABLE 1. Continued.

Organism	Structure created	Richness, S		Quadrat size†	Ecosystem	Reference
		On engineered patch	On unmodified patch			
Bison	wallow	5.2	11.8	0.1 m²	grassland, burned	Collins and Uno (1983)
Ant	mound	8	11.3	1 m²	dry alpine meadow	Culver and Beattie (1983)
Marmot	mound	7.4	14.5	0.25 m²	wet alpine meadow	del Moral (1984)
Marmot	mound	7.4	8.9	0.25 m²	dry alpine meadow	del Moral (1984)
Pocket gopher	mound	21	26	500 points	bunchgrass prairie	Williams and Cameron (1986)‡
Ant	mound	3.4	4.3	0.25 m²	pinyon pine–juniper grassland	Carlson and Whitford (1991)
Ant	mound	3.2	4.2	0.25 m²	ponderosa pine grassland	Carlson and Whitford (1991)
Curoro	burrow	27	31	30 m²	Chilean shrubland	Contreras and Gutierrez (1991)‡
Ant	mound	8.8	14.4	0.5 m²	mixed-grass prairie	Umbanhowar (1992)
Badger	mound	12	14.3	0.5 m²	mixed-grass prairie	Umbanhowar (1992)
Bison	wallow	10	12.3	0.5 m²	mixed-grass prairie	Umbanhowar (1992)
Woodchuck	burrow	2.6	3.4	0.25 m²	old field (Virginia, USA)	English and Bowers (1994)
Wild boar	grubbing	5.9	11.3	0.25 m²	California (USA) coastal grassland, 1 year post grubbing	Kotanen (1995)
Pocket gopher	mound	2.4	3.1	0.01 m²	tall-grass prairie	Rogers et al. (2001)
C) Studies in which engineer had no effect on species richness						
Badger	pit	17.4	16.4	0.2 m²	tall-grass prairie, ungrazed	Platt (1975)‡
Prairie dog	town	35	34	4 m²	mixed-grass prairie, town edge	Coppock et al. (1983)‡
Gerbil	burrow	12.6	12.1	1 m²	high-veldt grassland	Korn and Korn (1989)‡
Prairie dog	town	11	11.5	10 m²	mixed-grass prairie, two-year-old town	Cid et al. (1991)‡
Prairie dog	town	20.5	18	10 m²	mixed-grass prairie, three-year-old town	Cid et al. (1991)‡
Gopher	burrow	7.8	8.3	0.25 m²	serpentine grassland	Hobbs and Mooney (1991)
Ant	mound	24.5	22.4	n.a.	*Elyonurus muticus* savanna, spring	Lewis et al. (1991)
Kangaroo rat	burrow	11.8	11.6	0.25 m²	desert grassland	Heske et al. (1993)
Kangaroo rat	mound	2.4	2.4	0.25 m²	Chihuahuan Desert, inactive mounds, winter	Guo (1996)‡
Moose	open canopy	6.0	5.8	0.5 m²	boreal forest floodplain	Suominen et al. (1999)‡
Ant	mound	10.4	11	0.25 m²	pasture, Czechoslovakia	Kovar et al. (2001)
Beaver	meadow	60.8–79.3	65.4	60 m²	Adirondack riparian zones	Wright et al. (2002)

Note: Examples where differences in species richness were less than 10% are classified as having no effect.
† Studies that did not specify quadrat size are designated "n.a.".
‡ Study included data on productivity on and off engineered patch.

studies on the effects on species richness of commonly studied ecosystem engineers such as beaver, prairie dogs, termites, ants, gophers, wild boar, and structures such as mounds, burrows, trails, and wallows. We used the references from these articles to identify earlier studies for inclusion in the review. We included all studies that provided mean values for plant species richness of plots located on patches that had been modified by an ecosystem engineer and equal-sized plots located in unmodified areas in the same habitat. Studies that measured species richness in plots that combined both engineered and unmodified patches were excluded from the review since they estimate the effect of an ecosystem engineer at a spatial scale larger than the patch. Studies that used different-sized sample plots on and off engineered patches were excluded as well, since they could provide a biased estimate of the effect of ecosystem engineering due to species–area effects.

To test the quantitative predictions of the conceptual model, we identified the subset of studies that also contained data on productivity both on and off patches that had been modified by ecosystem engineers. In all cases, productivity was estimated as standing-crop biomass. While standing-crop biomass does not provide an exact

measure of primary productivity, it was the most commonly measured variable. Furthermore, most of the studies that measured standing-crop biomass occurred in grasslands, ecosystems where standing-crop biomass tends to provide a better estimate of primary productivity. We divided these studies into cases where ecosystem engineering created patches with higher productivity than unmodified patches and cases where engineered patches had lower productivity than unmodified patches. In order to standardize across the different plot sizes used to measure species richness in different studies, a proportional change in richness was calculated as: [(Mean richness on engineered patch) − (Mean richness off engineered patch)]/(Mean richness off engineered patch). For both data sets, we regressed the proportional change in richness against the productivity of unmodified patches using a linear regression to test whether the effect of engineering on species richness depended on the productivity of the system in which the engineer was active. This analysis also allowed us to determine if the direction of this relationship matched that predicted by the conceptual model, i.e., positive for ecosystem engineers that decrease productivity and negative for those that increase productivity.

RESULTS

Thirty-five studies contained data on the number of plant species found on patches that had been modified by ecosystem engineers and on unmodified patches of equal area, providing 60 separate measures of the effect of ecosystem engineers on patch-scale richness (Table 1). The studies took place in diverse terrestrial habitats, ranging from tundra to tropical grasslands, with most of the studies occurring in temperate and desert grasslands. The majority of ecosystem engineers studied were mammals, particularly mound-building mammals such as prairie dogs, kangaroo rats, pocket gophers, and marmots. However, the effects of ecosystem engineering by ants, herons, gopher tortoises, and desert shrubs on species richness also were investigated.

Ecosystem engineering had a wide range of effects on species richness (Fig. 2). In 28 out of the 60 cases the engineered patch showed a >10% increase in species richness relative to the unmodified patch. In 21 cases the engineered patch showed a >10% decrease in species richness relative to the unmodified patch, and in 10 cases there was a <10% difference in species richness between the two patch types.

Overall, there was little discernable pattern relating the effect on species richness at the patch scale to the identity of an ecosystem engineer, the type of habitat modification, or the ecosystem in which the engineer was active. Badgers, pocket gophers, and ants were all shown to increase, decrease, or have no effect on species richness. Boar were shown to increase and decrease richness and prairie dogs and kangaroo rats were shown to both increase and have no effect on richness. Ecosystem engineering in tall-grass prairie, Mediter-
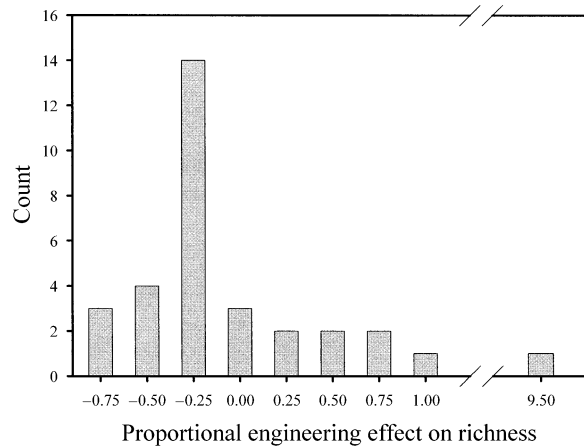

FIG. 2. Distribution of effect magnitudes of ecosystem engineering on species richness, as measured by proportional change in species richness between engineered and unmodified patches. ''Count'' = no. of reported measurements for each effect magnitude.

ranean grasslands, temperate forests, and old-fields all had positive, negative, and no effect on patch-scale species richness. Mounds, pits, and burrows sometimes increased species richness, sometimes decreased richness, and sometimes had no effect.

In contrast, the relationships between the effect of an engineer on productivity and its effect on species richness at the patch scale were quite striking. Fourteen studies reported data on both changes in species richness and productivity on and adjacent to patches that had been modified by ecosystem engineers, yielding 30 independent paired measures of richness and productivity (Table 2). Engineered patches had greater productivity than adjacent patches in the majority of these cases (24 out of 30 cases). These studies came from a narrower range of ecosystems than those contained in the full data set, but included productivity estimates for unmodified patches ranging from 3.4 to 554 g/m^2. A linear regression analysis showed a significant negative relationship between productivity in unmodified patches and proportional change in species richness ($P < 0.001$, df = 22, $r^2 = 0.26$) in cases where the ecosystem engineer increased productivity (Fig. 3). When productivity was lower in the engineered patch than in the unmodified patch, there was a weak positive relationship between productivity in unmodified patches and proportional change in species richness, although this relationship was not statistically significant ($P = 0.370$, df = 4, $r^2 = 0.203$) (Fig. 4).

DISCUSSION

Overall, published studies on the effects of ecosystem engineers on species richness at the patch scale support both the qualitative and quantitative predictions of our conceptual model. Engineer species identity, the type of habitat modification, and the ecosystem in which the

TABLE 2. Description of literature data showing the effects of ecosystem engineers on species richness and productivity at the patch scale.

Study	Richness, S			Biomass (g/m²)†			Comments
	On patch	Off patch	Quadrat size	On patch		Off patch	
A) Studies in which engineer increased productivity							
Platt (1975)	17.4	16.4	0.2 m²	494.3		302.6	virgin prairie
	15.3	12.0		528.2		271.2	overgrazed prairie
Fox (1985)	16.1	12.1	0.1 m²	215.6 (37.2)		113.7 (11.4)	
Williams and Cameron (1986)	16.0	17.0	500 points	507.1 (101)		447.5 (67.6)	
Guterman et al. (1990)	3.0	1.4	0.1 m²	134.1		21.0	
Contreras and Gutierrez (1991)	27.0	31.0	30 m²	111.1 (6.9)		69.7 (5.4)	
Boeken et al. (1995)	5.7	1.8	267 cm²	3.5 (0.40)		0.34 (0.08)	Drorim formation
	4.5	2.7		2.7 (3.48)		0.38 (0.08)	Upper Shivta formation
	6.7	4.1		5.1 (1.42)		0.71 (0.11)	Lower Shivta formation
	3.3	1.59		4.5 (1.20)		0.75 (0.40)	Nester formation
Guo (1996)	1.6	1.4	0.25 m²	289.6		64.6	summer, inactive mound
	2.6	1.8		78.6		75.9	summer, active mound
	2.4	2.4		349.0		90.5	winter, inactive mound
	4.6	2.6		173.8		120.9	winter, active mound
Boeken et al. (1998)	4.8	1.3	0.018 m²	134.1		21.0	south slope, low density
	6.5	2.6		374.4		82.4	south slope, medium-low density
	6.9	3.3		302.2		75.8	south slope, medium-high density
	5.9	2.8		533.4		91.9	south slope, high density
	4.4	2.3		184.8		33.7	north slope, low density
	4.6	2.0		67.3		28.4	north slope, medium-low density
	5.2	2.4		204.5		36.1	north slope medium-high density
	5.0	2.2		449.6		134.5	north slope, high density
Suominen et al. (1999)	5.8	6.0	0.5 m²	150.8 (24.1)		127.8 (18.7)	
Wilby et al. (2001)	12.9	4.4	0.4 m²	675.0 (120)		554.0 (10.0)	
B) Studies in which engineer decreased productivity							
Coppock et al. (1983)	39.0	34.0	4 m²	170.3 (17.7)		191.7 (15.7)	old patch
	45.0	34.0		94.3 (5.8)		191.7 (15.7)	young patch
	35.0	34.0		117.5 (7.8)		191.7 (15.7)	edge of patch
Cid et al. (1991)	11.0	11.5	10 m²	32.9		41.7	year 2
	20.0	18.5		96.8		131.1	year 3
Korn and Korn (1989)	12.6	12.1	1 m²	122.6		234.0	

† Biomass estimates are means (with 1 SE where available).

engineer was active showed no obvious relationship to the direction or magnitude of the effects of ecosystem engineering on patch-scale richness. On the other hand, knowing the productivity of unmodified patches and whether ecosystem engineers create patches with higher or lower productivity than unmodified patches allows a general prediction of the relative species richness of engineered and unmodified patches in some cases. This is encouraging given the broad array of methodologies and types of ecosystem engineers and environments covered in the data underlying the analyses.

The analysis of studies that measured both productivity and species richness on patches modified by ecosystem engineers vs. unmodified patches shows that the effect of engineering on richness potentially depends on both the productivity of the ecosystem and whether the ecosystem engineer increases or decreases productivity. In low-productivity ecosystems, engineering that results in patches with higher productivity than unmodified patches leads to patches with higher species richness, while engineered patches with lower productivity had lower species richness. In contrast, in
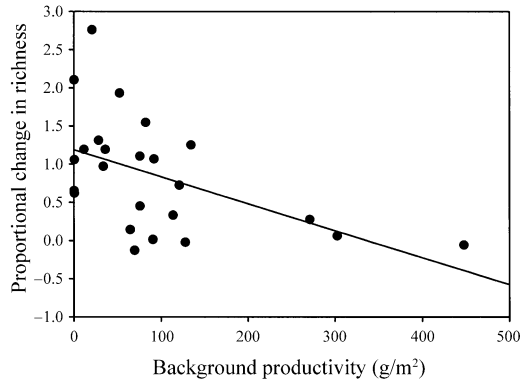
FIG. 3. Proportional change in species richness in patches modified by ecosystem engineering compared to unmodified patches along a gradient in the productivity of the unmodified patches for cases in which patches modified by ecosystem engineering had higher productivity than unmodified patches. The equation for the best-fit regression is $y = -0.004x + 1.19$. The proportional change is calculated as [(mean richness on engineered patches) $-$ (mean richness off engineered patches)] $\div$ (mean richness off engineered patches).

high-productivity systems, engineered patches with higher productivity have lower species richness, and those with lower productivity have higher richness than unmodified patches. While the data supporting these conclusions are limited and the relationship is not statistically significant when engineers decrease richness, the fact that the relationships are consistent with the predictions of the conceptual model is encouraging.

Although there was a significant relationship between the productivity of unmodified patches and the effect of ecosystem engineering on species richness when engineers increase productivity, productivity explained only 26% of the variance in the engineering effect on richness. In particular, there was considerable variability in the effect of ecosystem engineers in low-productivity systems in cases where ecosystem engineers increase productivity. Some of this variability may be due to variability in the ''intensity'' of engineering, or the degree to which engineered patches differ from the unmodified patches in productivity. One would predict that ecosystem engineers that create patches having very large effects on productivity would have proportionally larger effects on species richness at the patch scale.

Variability in the magnitude of the effect of ecosystem engineering on species richness also may be due to variability in plot size in the different studies. Plot sizes in the database ranged over more than two orders of magnitude. This is largely because different studies were sampling plant communities in patches created by different ecosystem engineers, and ecosystem engineers create patches at a wide range of spatial scales (Jones et al. 1994). Larger patches have a higher maximum number of individuals than smaller patches, and thus can have a higher potential range of richness values. We corrected for this discrepancy by looking at

the proportional change in species richness between engineered and unmodified patches, and by only selecting studies in which species-richness estimates for engineered and unmodified patches were determined from plots of equal size. Thus, the effect of the area of the sample on the observed relationship between ecosystem engineering and species richness should be minimized in these analyses.

There were relatively few cases where ecosystem engineered patches had lower productivity than unmodified patches, particularly in more productive environments. Whether this is because it is rare for ecosystem engineering to decrease productivity or rare for ecologists to study such systems is difficult to say. However, given the lack of data, the lack of a statistically significant relationship between primary productivity and the effects of engineers on richness when engineers decrease richness may be due to the low statistical power of the test. There also were fewer studies that reported both productivity and species richness on and off engineered patches in moderately to highly productive systems, regardless of whether engineering increased or decreased productivity. The paucity of data restricts our ability to draw strong conclusions, even though the existing data are consistent with the predictions of our model. Furthermore, determining the precise relationship between the effects of engineering on species richness and productivity would doubtless be improved by using better estimates of primary productivity than aboveground biomass. Aboveground biomass is the most commonly used proxy for primary productivity, and thus provided us with the most data points for analysis. However, it has clear limitations in ecosystems with large stores of perennial biomass and completely ignores the importance of belowground productivity. To further test the predictions of the conceptual model, more studies are needed comparing (1)
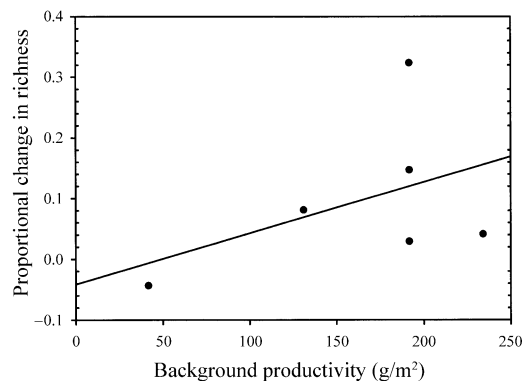

FIG. 4. Proportional change in species richness in patches modified by ecosystem engineering compared to unmodified patches along a gradient in the productivity of the unmodified patches for cases in which patches modified by ecosystem engineering had lower productivity than unmodified patches. The equation for the best-fit regression is $y = 0.001x - 0.002$. See Fig. 3 for calculation of proportional change.

the effects of the same ecosystem engineer on richness along productivity gradients, (2) the effects of different ecosystem engineers that create patches varying in productivity within the same ecosystem, and (3) studies with better estimates of primary productivity.

Comparisons to other models

Species rarely affect ecosystems via a single mechanism. Species that act as ecosystem engineers also can be important herbivores, predators, prey, producers, or decomposers. In some cases, it may be difficult to determine whether the effect of an organism on richness is due primarily to ecosystem engineering or herbivory or some other mechanism. Many of the mammalian species that were the focus of the studies reviewed here are also important herbivores, suggesting that the observed patterns may not be due solely to ecosystem engineering. The effects of ecosystem engineering by a particular species can often be more localized than the effects of herbivory by the same species. By restricting the review to studies that explicitly measured species richness on the mounds, pits, grubbings, or burrows created by ecosystem engineers, we increased the probability that the effects are at least in part due to ecosystem engineering. However, if a species modifies the habitat by creating a mound or a burrow and then acts as a central-place forager (Orians and Pearson 1979), the engineering effects and grazing effects of the herbivore might be largely coincidental in space (Wilby et al. 2001).

The results from the analysis of ecosystem-engineering effects on species richness at the patch scale show interesting similarities to the results of a recent meta-analysis of the effects of grazing on richness (Proulx and Mazumder 1998). Both studies found that the effect of the mechanisms of interest on species richness depended on the productivity of the ecosystem. Proulx and Mazumder (1998) found that grazing had a negative effect on species richness in low-productivity systems but tended to increase species richness in nutrient-rich systems, mirroring the results found here for ecosystem engineers that decrease productivity in modified patches. Since grazing also tends to remove biomass, the parallels between these two studies suggests that similar underlying ecological processes might be responsible for generating these patterns. Furthermore, herbivores often impact ecosystems through a variety of mechanisms in addition to grazing, including ecosystem engineering (Huntly 1991), and it may be that some of the putative grazing effects on species richness documented by Proulx and Mazumder (1998) were due to ecosystem engineering. The frequent conflation of the ecosystem-engineering effects of an organism with other effects, such as grazing, points out the importance of experimental studies that separate engineering from trophic effects to determine the relative importance of different mechanisms in controlling an organism's impact on the ecosystem (Boe-

ken and Shachak 1994, Crooks and Khim 1999, Rogers et al. 2001, Wilby et al. 2001).

The model presented here makes similar predictions to the model developed by Hacker and Gaines (1997) to predict the effect of facilitation on species richness. They suggest that positive interactions will increase species richness, but only in areas of low productivity or high physical stress. Assuming that positive interactions tend to increase productivity, their model predicts that in low-productivity ecosystems, species that create patches with higher productivity will lead to increased species richness. These predictions match those of the conceptual model presented here where ecosystem engineers that increase productivity in a low-productivity ecosystem should increase species richness. A key difference between these two models is that facilitation consists only of interactions in which both species benefit (Hacker and Gaines 1997), while ecosystem engineering can result in a broader spectrum of net effects.

Generality of our conceptual model

We have suggested that the effect of ecosystem engineering on plant species richness at the patch scale can be predicted if one knows the productivity of the ecosystem and whether modified patches have higher or lower species richness than unmodified patches. Because these predictions derive from a model based on basic ecological principles, they should hold when tested in ecosystems across a broad range of productivity, and with ecosystem engineers that modify the environment in different ways, given that a hump-shaped relationship between productivity and species richness holds. That said, the degree to which an ecosystem engineer affects species richness at the patch scale is likely to depend on a number of additional factors. The composition of the regional species pool could potentially have a large effect on the composition and richness of modified patches (Denslow 1980). If an ecosystem engineer is introduced into an ecosystem and creates patches with a combination of resources not previously present in the environment, few species may colonize the modified patch even if one might predict high numbers of species.

The model is also more likely to provide successful predictions of species richness when an ecosystem engineer modifies relatively few resource "flow chains" (sensu Shachak and Jones 1995), or the resources modified are all likely to have similar effects on species richness. Porcupine diggings in the Negev Desert have been shown to trap runoff, the primary factor limiting plant productivity (Gutterman et al. 1990), thereby increasing annual plant productivity (Boeken et al. 1995). Both patch types are colonized by a similar set of species, reflecting a common regional species pool. Consequently, porcupine diggings have a predictable positive effect on species richness in this low-productivity environment (Boeken et al. 1995). On the other hand,

beaver meadows have been shown to differ from forested riparian zones in light, soil moisture, and nitrogen levels (Naiman et al. 1994, Johnston et al. 1995), and the two patch types are colonized by very different sets of species, reflecting different species pools (Wright et al. 2002). In this case, ecosystem engineering modifies numerous resources in complex ways and results in engineered habitats that do not differ in species richness from unmodified habitat in any obviously predictable way.

CONCLUSIONS

Recognizing the importance of non-trophic interactions such as ecosystem engineering in controlling patterns of species richness is an important step in ecology. Not only are such interactions widespread, but, as shown here, they can be orderly and predictable using basic ecological principles. The effects of ecosystem engineering on species richness can appear idiosyncratic when viewed from the perspective of the identity of the engineer, the resources modified, the spatial scale and intensity of the modification, or the species responding. Nevertheless, knowing the productivity of engineered patches relative to unmodified patches allows a general prediction of how the effect of an ecosystem engineer on patch-scale species richness will vary along a productivity gradient. Such predictions are useful in understanding how the loss or introduction of species that act as ecosystem engineers might affect the distribution of species and ecosystem function across landscapes. Furthermore, the development and testing of conceptual models of ecosystem engineering, such as the one presented here, serve as an important step in moving the concept of organisms as ecosystem engineers toward a general ecological theory.

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CONCEPTS & SYNTHESIS