
Inherent Rarity in Community Restoration

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Abstract: *We explore the implications of an often overlooked fact in community restoration: most species, in real or synthetic communities, are infrequent or rare, a phenomenon we call "inherent rarity." Whether from long-term interactions of many factors affecting birth, death, and establishment within natural communities, or from short-term interactions of recently created communities, species abundance distributions are roughly lognormal or even more attenuated. The greater the predisturbance species diversity of remnants or the planting diversity of restorations, and the smaller the area of a habitat patch, the more likely a large proportion of species will exist in populations so small that they are acutely or chronically vulnerable to local extinction. We suggest that habitat fragmentation will inevitably favor plants and animals that are highly mobile, early successional species, including many exotic weeds among plants, or species that are historically organized as metapopulations that happen to be common enough to function as such. We further explore rationales for countering the effects of inherent rarity, including connectivity from buffers, corridors, and stepping stones, and dominance suppression from seasonally appropriate mowing, grazing, or fire.*

Rareza Inherente en la Restauración de Comunidades

Resumen: *Exploramos las implicaciones de un hecho que frecuentemente es pasado por alto en la restauración de comunidades: la mayoría de las especies, en comunidades reales o artificiales, son poco frecuentes o raras, un fenómeno que nosotros llamamos "rareza inherente". Ya sea por interacciones a largo plazo de muchos factores que afectan el nacimiento, la muerte, y el establecimiento en comunidades naturales, o por interacciones a corto plazo de comunidades recientemente creadas, las distribuciones de la abundancia de especies son apenas normales e incluso atenuadas. Cuanto más grande sea la diversidad de especies antes de una perturbación en remanentes o la diversidad de plantaciones en restauraciones, y cuanto menor sea el área de un parche de hábitat, mayor es la posibilidad de que una proporción grande de especies pueda existir en poblaciones tan pequeñas que estas sean agudas o crónicamente vulnerables a una extinción local. Nosotros sugerimos que la fragmentación del hábitat favorecerá inevitablemente a plantas y animales altamente móviles, especies de etapas sucesionales tempranas, incluyendo, entre las plantas, a muchas hierbas exóticas, o especies que históricamente se organizan en metapoblaciones y que son lo suficientemente comunes como para poder funcionar como tales. Exploramos también los fundamentos para contrarrestar los efectos de la rareza inherente, incluyendo a la conectividad con zonas de amortiguamiento, corredores y escalones, y la supresión de especies dominantes mediante el segado, pastoreo o incendios estacionales adecuados.*

Introduction

Ecological restorations of focal species and entire communities have different and sometimes contradictory assumptions. At its best, restoration of single-species populations creates stable habitat requirements or deter-

mines a set of manipulations or disturbances (e.g., fire regimens) required to maintain breeding populations of the animal or plant of concern (e.g., DeMauro 1994; Gogan & Cochrane 1994; Pavlovic 1994). On the other hand, community restoration recreates processes essential for maintenance of diverse, functional species assemblages (e.g., Jordan et al. 1987; Howe 1994a). An important—and to our knowledge largely overlooked—issue is that most species in a community are, for any number

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of reasons, infrequent or rare (Rabinowitz et al. 1986; Huston 1994; Howe 1999a). Restoration of focal populations, or focal populations and communities, may work at cross-purposes when management for one rare species or a community dominant creates conditions that put other infrequent or rare species at risk. We explore the implications for restoration ecology of what we call "inherent rarity," which is the property of all known communities that many or even most species are present in such small numbers that they are at risk of local extinction.

Species Abundance Distributions

Uneven distributions of species are a fundamental aspect of natural and restored communities. Preston (1948, 1962) first called attention to roughly log-normal species abundance distributions as a general feature of plant and animal communities in which a few species are common, some are found in intermediate and mostly low abundances, and many or most are rare. The characteristically left-skewed shape of the species abundance distribution is a likely consequence of many random factors influencing birth, death, and establishment of species within it (Magurran 1988). More recent interest in spatial self-similarity in species representation (Harte et al. 1999) echoes much earlier observations that clumping of individuals of rare species (Hairston & Beyers 1954; Hairston 1959) results in greater numbers of rare species than the log-normal distribution would predict.

The proportion of species in a community that are rare is in part determined by area. A comprehensive sample of a community has as many abundant as rare species (Preston 1948). A less comprehensive sample shows a preponderance of rare species (e.g., Fig. 1); progressively smaller sampling areas shift the mode of species abundance to the left (Fig. 2). In an example of rain-forest trees in a 50-ha plot chosen for topographic homogeneity, the modal number of individuals per species ranges from four to eight, whereas for smaller sampling areas the most common abundance category is one to two individuals per species (Hubbell & Foster 1983). If these were small habitat patches created by topographic relief, heterogeneous soils, historical drainage anomalies, or habitat islands, or if they were restorations instead of samples from continuous and homogeneous habitat, rare and uncommon subdominants would be highly vulnerable to chance local extinction (Appendix 1 in MacArthur 1972). In a landscape of anthropogenic fragments and restorations where species are neither extraordinarily vagile nor close to a source of immigrants, chance local extinctions are likely to result in permanent distortions of species composition in favor of abundant dominant or highly mobile subdominant species.

Among plants, dominance is related inversely to species diversity (Huston 1979, 1994). A short-term conse-

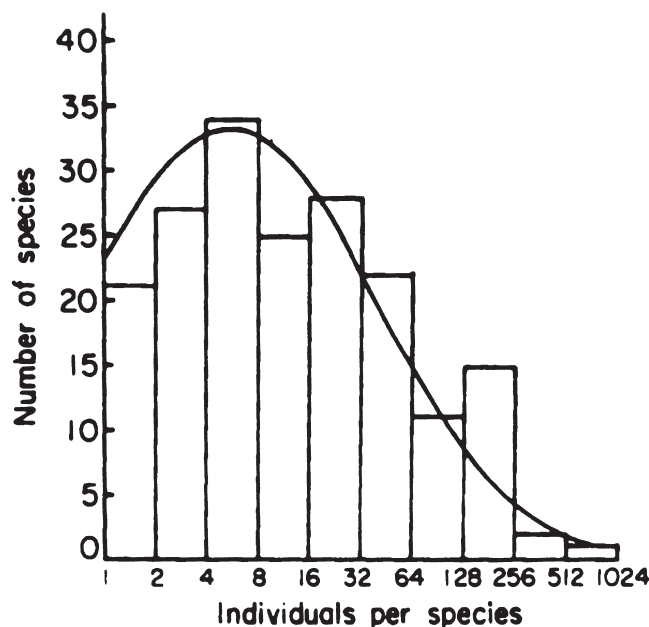


Figure 1. Lognormal distribution fitted to the relative species abundances of trees ≥ 20 cm diameter at breast height in a 50-ha plot on Barro Colorado Island, Panama (modified from Hubbell & Foster 1983). The site is a plateau of low topographic heterogeneity. Species are grouped into octaves of abundance.

quence of suppression of dominance is admission of interstitial subdominant species that otherwise would be excluded, thereby resulting in increased species diversity (Cornell & Lawton 1992). A long-term consequence could be replacement of one or more dominants by others, thereby resulting in reduction of diversity. We argue for variable management regimes that alternately suppress different dominants as one of the possible ways to maintain maximum species diversity in a given locale (Howe 1994a; Davison & Kindscher 1999). This may be the best way to maintain enough uncommon and rare species in large enough local populations to maintain dynamic interchange of species among habitat fragments.

Locally abundant or even common endemics could in principle occupy the populous end of the species abundance distribution in some places, but in general common species are dominants or smaller species that are abundant in most sites. Other subdominants may represent small breeding populations adapted to low abundance, small breeding populations suppressed by aggressive dominants, nonbreeding (i.e., sink) populations, or transients (Howe 1999a). Rabinowitz et al. (1986) defined several kinds of rarity based on geographic range, habitat specificity, and local population size (Table 1). In the flora of the British Isles, they found that 105 species could be categorized as "somewhere large" populations, but only eight could be categorized as "everywhere small" populations. If similar proportions are general in

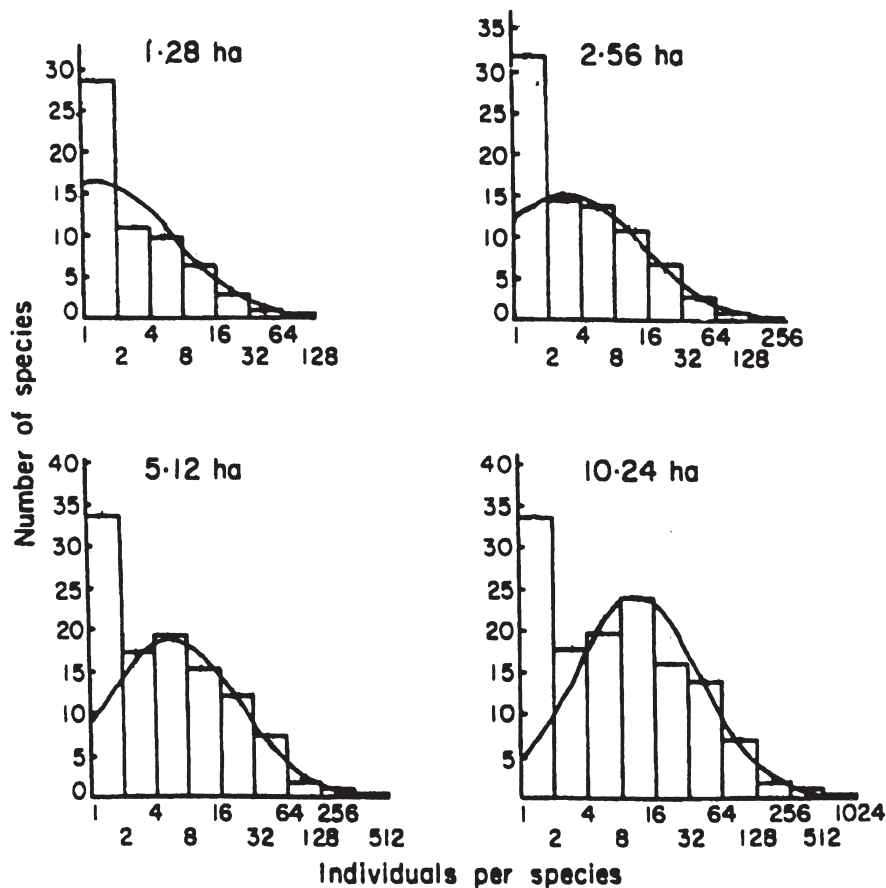


Figure 2. Progressive shift in the mode of the lognormal to the left one octave, with each halving of tree sample size in the range of 10.24 ha (256 quadrats 20 × 20 m) to 1.28 ha (32 quadrats 20 × 20 m) in subsamples of the 50-ha plot described in Fig. 1. Number of species in the one-individual-per-species octave was not used to fit the lognormal distribution. In a restored habitat patch, one expects a similar increase in the proportion of rare and infrequent species as habitat area declines or as diversity of the original patch increases. In a small restoration of initially high diversity, one expects the majority of species to become too rare to be self-sustaining. The rainforest figure is modified from Hubbell and Foster (1983).

other floras and faunas, two points need emphasis: (1) most rare or infrequent species in a log-normal species abundance distribution are probably derived originally from a “somewhere large population” species and (2) in most of the world populated by human cities and especially agriculture, most of the “somewheres” no longer exist.

Implications of Abundance

The ability of a species to persist in a habitat patch and to colonize vacant patches depends on abundance (MacArthur 1972). In addition, the ability of a species to

colonize new sites depends on the number of individuals and inherent characteristics, such as dispersal capacity as a seed, juvenile, or adult, that determine its overall vagility. The vagility of a species in turn determines whether the population is likely to be nonmobile but persistent or to behave as a metapopulation.

A metapopulation is a “population of populations” connected by occasional migration (Levins 1970; Hanski 1982; Murphy et al. 1990; Hanski & Gilpin 1991; McCullough 1996). Within local populations, there are finite probabilities of death through extinction and probabilities of birth through recolonization. At a global level, populations persist as long as effective recolonizations keep pace with local extinctions. Similarly, metapopula-

Table 1. Seven forms of rarity based on geographic distribution, habit specificity, local population size, and their likely relationships to species abundance distributions.*

Geographic distribution:	wide		restricted	
	broad	narrow	broad	narrow
Populations large somewhere	often dominant	usually subdominant	sometimes dominant	usually subdominant
Populations small everywhere	always subdominant	always subdominant	always subdominant	always subdominant

*From Howe (1999a); inspired by Rabinowitz et al. (1986).

tions in which rates of local extinction greatly exceed rates of recolonization are doomed in the long term, although isolates may persist without migration as long as environmental and demographic conditions permit.

Not all species behave like metapopulations (Doak & Mills 1994). In continuous habitats, for example, the spatial structure integral to metapopulations may be absent, or mobile organisms may act as continuous populations even if local populations appear spatially distinct. Alternatively, species that once existed in continuous populations may not be mobile enough to consistently re-colonize vacant sites created during the course of anthropogenic habitat fragmentation or restoration. Such apparent but unreal "metapopulations" may experience much higher rates of local extinction than of recolonization, such that the persistence of small, peripheral subpopulations are of short duration.

Further, mobile dominant species are likely to be common enough to function as metapopulations, as are some particularly vagile subdominant species. Most subdominant species, however, are likely to be so uncommon or so sedentary that they do not function as metapopulations capable of following local extinctions with consistent recolonizations. If 50–70% of the species in a habitat patch are at the scarce end of the species abundance distribution or are not inclined to migrate consistently from one patch to another, inexorable local extinction will open spaces that will tend to be occupied by species that are (1) historically organized as metapopulations, (2) so vagile that local groups of individuals are really part of panmictic populations, (3) highly vagile members of early successional communities, including opportunistic weeds, or (4) abundant local species released from competition.

One expects a shift of the mode of the species abundance distribution to the right as uncommon species are lost and replaced by more abundant counterparts. Potential ramifications may go beyond species counts if some species strongly influence the ability of others to survive and reproduce. For instance, Barro Colorado Island was separated from the mainland during the building of the Panama Canal in 1914. A survey of birds in 1970 (Willis 1980), with fruit-eating species graphed as a species abundance distribution (Fig. 3), shows a highly abnormal deficit of uncommon species, suggesting a disproportionate loss of uncommon species and perhaps ecological release of abundant species. One expects species with longer generation times, such as trees, to follow suit, especially if missing frugivores once served as key dispersal agents.

Prescriptions

If we are correct, most members of most species abundance distributions in fragmented remnants or restora-

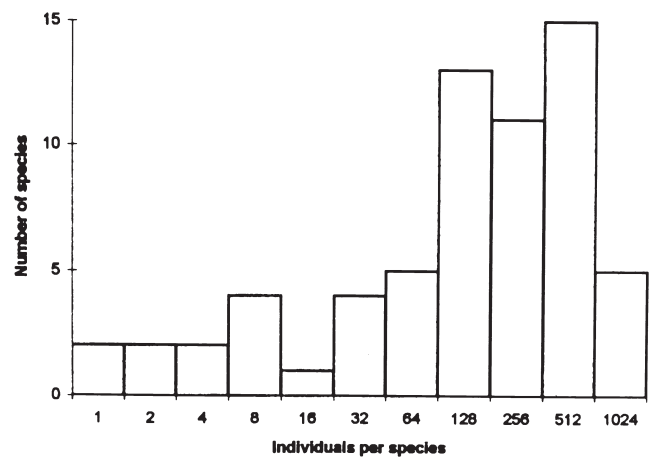


Figure 3. Relative abundances of fruit-eating birds on Barro Colorado Island, Panama, surveyed in 1970 by Willis (1980) (modified from Howe 1984). This highly atypical distribution suggests loss of rare and infrequent species.

tions are at risk. One expects attrition of such species and their replacement by more vagile taxa historically organized as metapopulations (some invasive "weeds") or competitive releases of common core species with a concomitant decline in species diversity. Countermeasures may have to be imposed on a system-by-system basis. Enforced habitat connectedness could lessen such losses by permitting metapopulation processes to continue or begin. Manipulation of species abundance distributions through suppression of dominance may also lessen such losses without providing corridors for invasive species, but it could provide unwanted opportunities for opportunistic weeds already present. The question then becomes whether desired species suffer more from direct suppression by dominants or from diffuse competition from invasives. Where connectedness or dominance suppression fail to maintain subdominant populations, uncommon subdominants may have to be added to counter local extinction.

Connectivity among habitat patches encourages metapopulation longevity (Hess 1996; McCullough 1996). This also is true of restoration, with the added proviso that many restored habitat buffers, corridors, and stepping stones will facilitate movement of plants and animals among remnant and recreated patches (Janzen 1988). Connectivity does allow interchange of mobile birds and mammals among patches (Arnold et al. 1991; Anders 1994) and may promote migration and gene exchange among the most mobile plants and invertebrates (Saunders et al. 1991). For instance, dispersing bighorn sheep (*Ovis canadensis*) make free use of both habitat corridors and isolated habitat islands too small to support a population as both avenues and resting sites (Bleich et al. 1996). Such highly mobile species are likely to make the best use of conserved or re-created habitat commu-

nities, buffers, corridors, and stepping stones. Connectivity may also promote movement of highly vagile invasive species which may be problematic in habitats encountering frequent disturbance.

Less mobile species at the infrequent and rare end of species abundance distributions will not be so fortunate. Even among relatively mobile taxa, such as birds, passive connectivity by itself may not maintain historical species abundance distributions. For instance, Maina (1993) found that generalist bird species freely used rehabilitated habitat patches ranging in size from 10 to 250 ha in and near the Baringo Fuel and Fodder Project in Kenya, but many nectarivores and frugivores did not (cf. Fig. 3). Much as local extinctions of key mutualists could lead to widening circles of extinction of interdependent plants and mutualists in remnant communities (Howe 1977, 1984), the absence of pollinators and dispersal agents in habitat restorations intended to serve as buffers, corridors, or stepping stones could well prevent colonization of those patches by dependent plants and thereby preclude establishment of viable populations.

We argue that the isolation or restoration of communities creates a tension between populations historically organized as metapopulations and those that are not. With proper habitat corridors, habitat stepping stones, and buffers, species historically organized as metapopulations may persist indefinitely. Without special measures, species not historically organized as metapopulations will be lost and may be replaced by more mobile native or exotic species. One expects shifts in community composition in favor of species historically organized as metapopulations and other vagile species, including exotic weeds.

Much as fisheries have suffered from standardized policies of maximum sustained yield (Ludwig et al. 1993), restoration may suffer from standardized methodologies that over time may tend to fix rankings of species within species abundance distributions. An example is management of tallgrass prairie, arguably the most endangered major ecosystem in North America (Noss et al. 1995). Eastern prairie remnants are generally protected from grazing and are burned in fall or spring to limit incursions of trees and shrubs (e.g., McClain 1986; Collins & Wallace 1990), thereby maintaining a higher diversity of prairie plants (Leach & Givnish 1996). But in favoring aggressive C_4 grasses, fall or spring burns may reduce the diversity of C_3 grasses and forbs (Higgins 1984; Howe 1994a, 1994b, 1995) and the insects that depend upon them (Swengel 1994, 1996; Swengel & Swengel 1997). Varied burn schedules and varied schedules of light to moderate grazing should in theory depress these aggressive dominants (Huston 1979; Cornell & Lawton 1992), thereby favoring different taxa among the infrequent members of the species abundance distribution, leading to spatial and temporal variability in the relative abundance of uncommon or rare subdominant species (e.g., Collins 1987; Howe 1999a, 1999b; Davison & Kindscher

1999). Such manipulation of species abundance distributions should, over time, increase opportunities for subdominant species to establish local populations in some habitat patches and for different sets of subdominants to take advantage of buffers, corridors, or stepping stones maintained by conservation or created through active restoration.

Enforced connectedness and dominance suppression may still fail to encourage uncommon and rare species that are not historically organized as metapopulations to function as metapopulations. The need for continued augmentation will be greatest in attempts to restore entire communities, habitat buffers, corridors, and stepping stones because ecological restorations virtually always harbor a much smaller subset of species than remnants of the same size and physical properties (e.g., Maina 1993; Howe 1994b, 1995; Galatowitsch & van der Valk 1996). It follows that exclusion through precedence of dominant species, subdominants adapted for metapopulation existence, and early successional pioneers or weeds will be more rapid in restored than remnant habitats.

Conclusions

The assumption in restoration ecology that if a habitat is created then colonists will come (Palmer et al. 1997) may apply to some species far more than others. It may predict consistent metapopulation dynamics among generalist or early successional species common on habitat edges or those species historically organized as (and common enough to function as) metapopulations. We expect that passive connectivity will be insufficient to ensure colonization of restored buffers, corridors, or stepping-stone habitats by subdominant species that are neither vagile, common, nor widely distributed. The sobering prediction is an inexorable shift in species composition in favor of abundant or early successional plants and animals and species historically organized as metapopulations.

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