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Contributed Paper

Taxonomic and Geographic Patterns of Decline for Threatened and Endangered Species in the United States

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Abstract: *Species listed under the U.S. Endangered Species Act (i.e., listed species) have declined to the point that the probability of their extinction is high. The decline of these species, however, may manifest itself in different ways, including reductions in geographic range, number of populations, or overall abundance. Understanding the pattern of decline can help managers assess extinction probability and define recovery objectives. Although quantitative data on changes in geographic range, number of populations, and abundance usually do not exist for listed species, more often qualitative data can be obtained. We used qualitative data in recovery plans for federally listed species to determine whether each listed species declined in range size, number of populations, or abundance relative to historical levels. We calculated the proportion of listed species in each state (or equivalent) that declined in each of those ways. Nearly all listed species declined in abundance, and range size or number of populations declined in approximately 80% of species for which those data were available. Patterns of decline, however, differed taxonomically and geographically. Declines in range were more common among vertebrates than plants, whereas population extirpations were more common among plants. Invertebrates had high incidence of range and population declines. Narrowly distributed plants and invertebrates may be subject to acute threats that may result in population extirpations, whereas vertebrates may be affected by chronic threats that reduce the extent and size of populations. Additionally, in the eastern United States and U.S. coastal areas, where the level of land conversion is high, a greater percentage of species' ranges declined and more populations were extirpated than in other areas. Species in the Southwest, especially plants, had fewer range and population declines than other areas. Such relations may help in the selection of species' recovery criteria.*

Keywords: endangered species, Endangered Species Act, extinction risk, recovery plans, species declines

Patrones Taxonómicos y Geográficos de la Declinación de Especies Amenazadas y en Peligro en los Estados Unidos

Resumen: *Las especies incluidas en el Acta de Especies en Peligro de E.U.A. (i. e., especies enlistadas) han declinado hasta el punto en que su probabilidad de extinción es alta. Sin embargo, la declinación de estas especies se puede manifestar de manera diferentes, incluyendo reducciones en el rango geográfico, el número de poblaciones o la abundancia total. La comprensión del patrón de declinación puede ser de utilidad para que los manejadores evalúen la probabilidad de extinción y definan objetivos de recuperación. Aunque generalmente no existen datos cuantitativos sobre los cambios en distribución geográfica, el número de poblaciones y la abundancia de especies enlistadas, se pueden obtener datos cualitativos. Utilizamos datos cualitativos de planes de recuperación de especies enlistadas federalmente para determinar si cada especie enlistada declinó en su rango de distribución, número de poblaciones o abundancia en relación con niveles históricos. Calculamos la proporción de especies enlistadas en cada estado (o equivalente) que declinaron en cada una*

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de esas formas. Casi todas las especies enlistadas declinaron en abundancia, y el rango de distribución o el número de poblaciones declinó aproximadamente en 80% de las especies de las que se disponía de datos. Sin embargo, los patrones de declinación difirieron taxonómica y geográficamente. Las declinaciones en rango fueron menos comunes en plantas que en vertebrados, mientras que las extirpaciones de poblaciones fueron más comunes en vertebrados. Los invertebrados tuvieron una alta incidencia de declinaciones en rango de distribución y poblaciones. Plantas e invertebrados con distribución restringida pueden estar sujetas a amenazas graves que reducen la extensión y tamaño de las poblaciones. Adicionalmente, en el este de Estados Unidos y en las áreas costeras de E.U.A., donde el nivel de conversión de tierras es alto, declinó un mayor porcentaje de los rangos de distribución y fueron extirpadas más poblaciones que en otras áreas. Especies en el suroeste, especialmente plantas, tuvieron menos declinaciones en rango y población que en otras áreas. Tales relaciones pueden ayudar a la selección de criterios para la recuperación de especies.

Palabras Clave: Acta de Especies en Peligro, declinación de especies, especies en peligro, planes de recuperación, riesgo de extinción

Introduction

Species listed as threatened and endangered under the U.S. Endangered Species Act (ESA) have high probabilities of extinction (Wilcove et al. 1993). The type of decline, including declines in geographic range, number of populations, and overall abundance, may vary considerably among species. Extinction can result from any single type of decline, but at some point along the trajectory to extinction all types occur simultaneously. At early and intermediate stages of decline, however, understanding the nature of decline may help halt or reverse decline (Neel 2008). In studies of threatened and endangered species in the United States, taxonomic composition, geographic distribution, and threats have been examined (Flather et al. 1994, 1998; Dobson et al. 1997; Wilcove et al. 1998; Rutledge et al. 2001). Building on these efforts, we conducted the first comprehensive analysis of ways in which species listed as threatened or endangered under the U.S. ESA are declining.

The demographic and genetic factors that increase the probability of extinction associated with decreases in abundance are different from the factors that affect the probability of extinction associated with range contractions or population extirpations (henceforth, extirpations). Declines in abundance can increase the effects of demographic stochasticity (Lande 1998) and Allee effects (Allee 1931) and increase levels of inbreeding, which reduces survival and reproductive success (Wright 1931; Kimura & Crow 1964; Nei & Tajima 1981). Species with historically large populations that abruptly decline in abundance have a particularly high probability of extinction (Holsinger & Vitt 1997).

The genetic consequences of extirpations and range contractions are less predictable than those of declines in abundance (Neel 2008). If reductions in range size reduce the breadth of environmental gradients occupied by a species, local and potential for future adaptation may be reduced (Moritz 2002). Nevertheless, the magnitude of such effects varies across species as a function of the genetic differentiation among populations and distribution of locally adapted traits. These losses in genetic diversity do not directly affect levels of inbreeding in remaining populations, unless extirpations increase the geographic distances among remaining populations. In this case movement that facilitates gene flow among populations (i.e., connectivity) can be disrupted.

Range contractions (Channell & Lomolino 2000a, 2000b; Hemerik et al. 2006), extirpations (Hanski et al. 1995; Neel 2008), and the interaction of these 2 factors increases the immediate probability of extinction by reducing the range of environmental variation in locations occupied by the species (Reed 2004). Traditionally, the distributions of species were thought to contract from the edges toward the core of their range, where they were assumed to have the greatest fitness (Brown 1984; Whittaker et al. 2005). Alternatively, Channell and Lomolino (2000a, 2000b) contend that a threat spreading across a landscape results in ranges contracting toward the periphery farthest from the threat. Although the pattern of range contractions affects whether conservation actions should focus on core versus peripheral populations, either type of contraction increases the similarity of environmental variables among sites, which can increase the negative effects of stochastic events (e.g., a hurricane).

The types of declines associated with a particular species are usually a function of intrinsic species' traits, extrinsic threats, and their interaction. Biological traits (e.g., body size, longevity, range size) generally are more similar within than among taxonomic groups (e.g., birds, insects, plants), which is thought to result in similar vulnerabilities within a taxonomic group to extinction from particular threats. For example, many mammals and birds occupy relatively large areas and have low-density populations. Reductions in the overall abundance of such wide-ranging species may result in range contractions without extirpations. In contrast, threatened and endangered plants and invertebrates are often endemic to small areas and have discrete high-density populations. Such populations can be more easily extirpated, but unless a population is in the periphery of the species' range, the overall range of the species is not reduced during the initial phases of decline. Range size and population density can then interact with extrinsic threats, which in turn are often clustered geographically (Flather et al. 1994, 1998). For example, in parts of the western United States, many threats to species may be related to changes in disturbance regimes caused by grazing by domestic livestock and water diversions (Flather et al. 1998). Such threats could result in declines in abundance without causing extirpations or range reductions.

Understanding the patterns of species declines can help guide recovery efforts. For species listed under the ESA, the Secretary of the Interior is required to develop a recovery plan that outlines the management actions needed for the conservation and survival of a species, unless the Secretary finds that such a plan will not promote conservation of the species (16 U.S. Code, section 1533[f][1]). Recovery plans specify objective measurable criteria, such as the number or size of populations, extent of habitat or range, and the spatial arrangement of populations (Wilcove et al. 1993; Tear et al. 1995; Gerber & Hatch 2002; M.C.N, unpublished data). We believe understanding the nature of declines for specific species can help ensure that these recovery objectives are appropriate.

Detailed quantitative data on the distribution and population size trends of species are the preferred basis for defining scientifically defensible recovery objectives because such data can be used to assess the probability of extinction. Evaluations of recovery plans indicate the status of a threatened or endangered species may be more likely to improve if recovery criteria are clearly linked to species biology (Gerber & Hatch 2002). Although the number of recovery criteria included in plans increased in the 1990s, proportionally fewer were quantitative and fewer had a clear connection to species biology (Gerber & Hatch 2002). The shift away from quantitative, biologically linked recovery criteria, however, may have resulted from a lack of available data because information on the status of species can be difficult, costly, and time consuming to gather.

In contrast to quantitative assessments of status, the qualitative status of a species is frequently known. For example, the natural extent of a species range may be unknown, but it may be known that the range has declined over time. Nevertheless, qualitative data on range contractions, extirpations, and reductions in abundance are often not explicitly acknowledged as sources of information and can easily be overlooked when formulating recovery strategies. In the absence of quantitative data, it seems reasonable to implement conservation strategies that ameliorate the type of decline a species is experiencing. Moreover, if there is spatial or taxonomic concordance in declines, more general regional strategies for threat alleviation could be developed for species that occur in the same region. We evaluated the qualitative type of decline for species listed under the ESA and examined the proportion of species that declined in range, number of populations, and overall abundance and through a combination of these types of decline. We then examined how the prevalence of these types of decline varied among 3 broad taxonomic groups (invertebrates, vertebrates, and plants) and 11 more finely resolved taxonomic groups. Additionally, we examined the association between patterns of decline and geography.

Methods

Determination of Species and Recovery Plans Analyzed

Our primary interest was in domestically listed species for which recovery plans have been approved. In the United States, species and subspecies of all plants and animals and distinct populations segments of vertebrates can be listed under the ESA. We refer to these as recovery entities. Our recovery entities largely correspond to those provided by the National Marine Fisheries Service (NMFS) and the U.S. Fish and Wildlife Service's (FWS) Threatened and Endangered Species Database System (TESS). In some cases, however, we treated a species as more than one recovery entity if it was treated as such during the recovery planning process, despite how it was treated in TESS or by NMFS. For example, the agencies treat the loggerhead sea turtle (*Caretta caretta*) as a single entity. Nevertheless, there are separate recovery plans with different objectives for the species in the Atlantic and Pacific. In another example, the FWS treats *Achatinella* snails in Hawaii as a single listing unit. Nonetheless, the Federal Register listing rule (FWS 1981) covers 41 species of *Achatinella*, and the recovery plan for the genus includes separate range maps and historic and extant locality information for each species. We therefore treated the genus *Achatinella* as 41 recovery entities.

We examined recovery entities that occurred in the 50 states, District of Columbia, U.S. Virgin Islands, Commonwealth of Puerto Rico, Territory of Guam, Commonwealth of the Northern Mariana Islands, and Territory of American Samoa. For each recovery entity, we collected data from the latest recovery plans approved as of 31 December 2009. We excluded recovery entities that were delisted due to taxonomic error or because new information had been discovered or had a recovery plan before being federally listed. We excluded 6 marine species, white abalone (*Haliotis sorenseni*), 4 whales, and 1 marine plant (*Halophila johnsonii*), from our analyses because their life cycles do not include use of terrestrial or freshwater ecosystems. Threats to these species are very different from threats to terrestrial and freshwater species, and these species could not be clearly associated with a state or equivalent in the geographic analysis. The total number of recovery entities we analyzed was 1164.

Type of Decline for Recovery Entities

For each recovery entity, we determined from the final approved recovery plan whether the domestic range, number of populations, or abundance was the same or smaller at the time the recovery plan was written relative to historic levels. We considered the historic status of a recovery entity its extent, distribution, and abundance prior to human activities (actual or proposed) or occurrence of natural phenomena that reduced the entity's probability of persistence to the point that the listing process was initiated. Recovery plans are the only documents that provide a synoptic assessment of status that is relatively standard across all threatened or endangered species. Data from other sources, such as the peer-reviewed literature, gray literature, or assessments by conservation organizations, may have provided different data (or, more likely, additional data), but collecting such information was beyond the scope of our study.

Our definition of historic is not associated with a given time because the date when human activities or other environmental changes became threats varies across species and is often unknown. The historic status and time period discussed in recovery plans varied across recovery entities. In cases where this time span was long, conservation actions may have been implemented that improved a recovery entity's status. We considered only the way in which a recovery entity declined, not improvements in status due to recovery actions. We calculated the percentage of recovery entities associated with a type of decline and made no inferences about the magnitude of such declines for individual recovery entities.

We considered qualitative data on range size, number of populations, and abundance of a recovery entity only if a recovery plan explicitly stated that these values were equal or less than historic values. If a plan did not include clear information on range size, number of populations, or abundance, we recorded the data as "not specified." When assessing the range of a species, we considered its geographic extent of occurrence, not its area of occupancy. Therefore, if the recovery plan indicated the "distribution" of a recovery entity decreased, but did not otherwise indicate the range decreased, we did not assume a range contraction. We defined a population of a recovery entity as it was defined in the recovery plan. If the definition of a population was unclear, we used criteria from the recovery objectives to guide our definition. Although our definition of a population is loose, we believe it is sufficient for our purposes. We defined abundance as the overall number of individuals of a species.

We recorded whether recovery plans included quantitative or qualitative data for each type of decline. We considered quantitative data available only if both historic and current (at or around the time the plan was written) values were provided.

Taxonomic Patterns of Decline

We aggregated recovery entities into 11 taxonomic groups used by the FWS (Table 1) and calculated the proportion of recovery entities in each group (with available data) associated with each type of decline. We then consolidated the 11 taxonomic groups into 3 categories—vertebrates, invertebrates, and plants—and calculated the proportion of recovery entities in each of these groups associated with each type of decline. After eliminating arachnids from the analysis because of their small sample size, we used a 10×2 contingency table to test for differences in type of decline among taxonomic groups and a 3×2 contingency table (including data from arachnids) to test for differences among vertebrates, invertebrates, and plants. We conducted these analyses separately for declines in range and number of populations. Nearly all recovery entities declined in abundance, so we did not analyze these declines further.

We had no way to determine whether declines in range, number of populations, and abundance occurred simultaneously or sequentially. Nevertheless, in cases when both the qualitative range and number of populations were known for recovery entities, we used a 2×2 contingency table to examine their joint distribution among taxonomic groups and among vertebrates, invertebrates, and plants.

Geographic Patterns of Decline

We collected data from TESS on the historic distribution of recovery entities at the state or equivalent (e.g., territory, commonwealth) level. When these data were not available, we used the FWS or NMFS website and the recovery plan for the entity to delineate its geographic extent. Although finer-resolution data on historic distribution were available for some species, we used state-level data because they were the data most consistently available for many recovery entities.

We calculated the proportion of recovery entities within a state or equivalent for which ranges had contracted or populations were extirpated. We considered a recovery entity had declined in a state or equivalent if it had declined anywhere within its range (even if it had not declined in that state or equivalent). Because taxonomic group was associated with the proportion of recovery entities for which both range size and number of populations had declined and because there was a geographical difference in the taxonomic distribution of recovery entities (e.g., more invertebrates in the southeast, more plants in Hawaii and California), we calculated range and population reductions separately for vertebrates, invertebrates, and plants.

Table 1. Qualitative data for range contractions, population extirpations, and declines in overall abundance for taxa listed as threatened or endangered under the U.S. Endangered Species Act.

		Range			Population			Abundance		
Taxonomic group	Recovery entities analyzed[a]	recovery entities with data[b]	reduced	same	recovery entities with data[b]	reduced	same	recovery entities with data[b]	reduced	same
Vertebrate	325	231	185	46	231	149	82	261	258	3
amphibian	17	14	5	9	15	10	5	9	9	0
bird	100	70	60	10	65	39	26	89	88	1
fish	110	89	75	14	90	67	23	84	82	2
mammal	59	37	35	2	40	26	14	50	50	0
reptile	39	21	10	11	21	7	14	29	29	0
Invertebrate	196	153	134	19	155	137	18	91	91	0
arachnid	6	1	1	0	2	2	0	1	1	0
clam	69	51	51	0	51	51	0	20	20	0
crustacean	18	12	5	7	14	9	5	2	2	0
insect	34	23	20	3	27	23	4	14	14	0
snail	69	66	57	9	61	52	9	54	54	0
Plant	643	487	350	137	547	455	92	390	383	7
All recovery entities	1164	871	669	202	933	741	192	742	732	10

[a] *Includes species, subspecies, and distinct population segments for which final recovery plans have been approved (see Methods).*
[b] *For each category of decline, sample sizes differed because recovery entities for which the information was not specified, unknown, or unclear were excluded.*

Results

We reviewed 599 recovery plans that included 1164 recovery entities (Table 1). Qualitative data on change in abundance, range size, and number of populations were available for 64% ($n = 742$), 75% ($n = 871$), and 80% ($n = 933$), respectively, of recovery entities. Qualitative data on all 3 types of declines were available for 45% ($n = 526$) of recovery entities and no data on any type of decline were available for 7% ($n = 85$) of recovery entities. Four percent of recovery plans ($n = 42$) had quantitative data on both the historic and current range size of recovery entities and 2% of recovery plans ($n = 28$) had data on abundances. For approximately half the recovery entities (49%, $n = 566$), the number of historic and current populations was available. Of the recovery entities with qualitative data available, a considerable majority had declined in abundance (99%), range size (77%), and number of populations (79%) (Table 1).

Taxonomic Patterns of Decline

The 10 taxonomic groups and the 3 taxonomic categories differed significantly in the proportion of recovery entities with declines in range and extirpations (Table 2, Figs. 1 & 2). Generally, fewer plants (72%, $n = 497$) than vertebrates (79%, $n = 231$) declined in range, but extirpations were more prevalent among plants (83%, $n = 547$) than vertebrates (64%, $n = 231$). Invertebrates had the greatest percentage of range contractions and extirpations (88% in each category, $n = 153$ for range, $n = 155$ for populations).

Declines in range and number of populations were not independent (Table 3). Many (74%) recovery entities had a reduction in both range and number of populations, whereas nearly 17% had neither. About 8% of plants had extirpations without decreases in range size, whereas <3.5% of other taxa exhibited this pattern (i.e., populations were extirpated from the central portions of their ranges). About 14% of vertebrates had range contractions without extirpations. For several taxa (e.g., crustaceans, amphibians, and reptiles), the expected values for an individual cell were <5; thus, significant values should be interpreted with caution.

Geographic Patterns of Decline

For the 3 taxonomic categories of recovery entities, geographic patterns of range contractions and extirpations were somewhat correlated (Fig. 3). Overall, recovery entities in the southwest had a lower proportion of range and population declines relative to those in the eastern United States and California. Generally, plants followed

Table 2. Comparison of the prevalence of range contractions and population extirpations among all taxa and 3 broad taxonomic groups.

	df	χ^2	p
Range contraction			
all taxa*	9	70.83	<0.001
invertebrate/vertebrate/plant	2	18.03	0.001
Population extirpation			
all taxa*	9	71.85	<0.001
invertebrate/vertebrate/plant	2	43.81	<0.001

**Arachnids removed from analysis because of small sample size.*

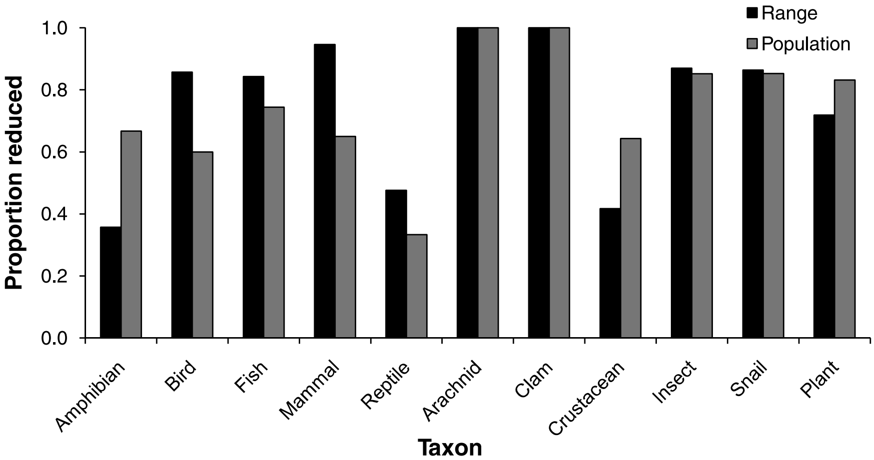

Figure 1. Proportion of recovery entities (species, subspecies, and distinct population segments), for which final recovery plans have been approved, with range contractions or population extirpations, by taxonomic group. Sample sizes are in Table 1.

this trend, but vertebrates had a higher proportion of range and population declines in the southwest. Invertebrates had a high prevalence of range contractions and extirpations regardless of their location.

Discussion

The pervasiveness of declines in range, number of populations, and abundance are to be expected for imperiled species. Nevertheless, the patterns of decline and the association of these patterns with taxonomy and geography can inform recovery planning.

Taxonomic Patterns of Decline

Range contractions and extirpations were common to the majority of listed species, but exceptions highlight the effects of the interaction of geography and range sizes. For example, a relatively small percentage of listed crustaceans had declines in range (42%), number of populations (64%), and both factors combined (33%), possibly because they are naturally rare (Fig. 1 & Table 3). Extirpations and range contractions had not been documented for 5 crustaceans. Four of these 5 species are restricted to caves and were listed under the ESA in part due to their restricted range. Similar to the endangered crustaceans, but in contrast to most vertebrates, range contractions (48%), extirpations (33%), and both factors combined (19%) were relatively rare among reptiles (Fig. 1 & Table 3). Three reptiles are endemic to Mona or Monito (small, uninhabited islands on the western edge of the Puerto Rican archipelago), and 1 is endemic to the Channel Islands in California. All 4 are threatened by the presence of non-native species that reduce the quality of their habitat and prey on them.

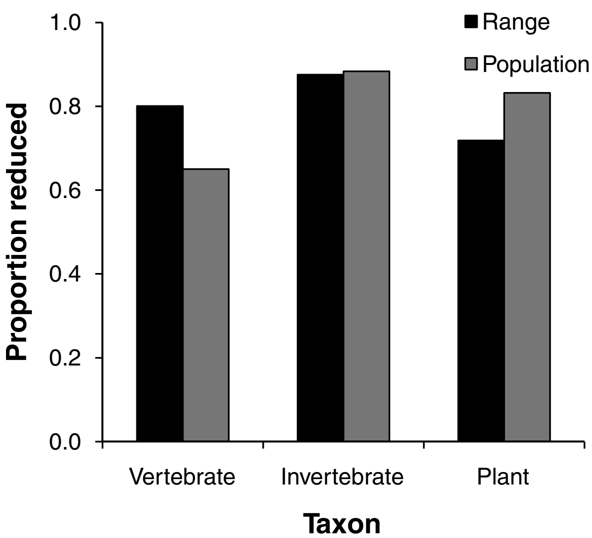

Figure 2. Proportion of vertebrates, invertebrates, and plants for which range contractions and population extirpations were documented in recovery plans. Sample sizes are in Table 1.

Plants and vertebrates had different combinations of range contractions and extirpations, which in turn would affect conservation recommendations. Nearly 8% of plants had extirpations without range contractions, in contrast to 3% of vertebrates (Table 3). These plants are losing populations from the central portion of their range, which could alter levels of connectivity among remaining populations. In contrast, 14% of vertebrates, but <1% of plants, had range contractions without accompanying extirpations (Table 3). Threats to vertebrates often may be more concentrated at the periphery of their ranges, but are not so intense that populations are extirpated. Unlike plants, whose geologic or fine-resolution environmental associations often result in dense, geographically circumscribed populations, many vertebrate populations are relatively diffuse and widespread, which may provide a buffer against extirpations. We could not rule out the possibility that ranges of vertebrates are contracting toward one side of their range rather than the core. In either of these cases, species no longer are present at the periphery of their former ranges, where they may have adapted to local environmental conditions. Loss of

Table 3. Results of contingency-table analysis of combinations of range contractions and population extirpations, within each taxonomic group, for cases in which the status of both types of decline were known.

	Range reduced, population extirpations	*Range reduced, no population extirpations*	*Range same, population extirpations*	*Range same, no population extirpations*	*df*	χ^2	p
Vertebrate	118	25	6	34	1	62.17	<0.001
amphibian	5	0	2	5	1	3.54	0.06
bird	35	10	0	8	1	15.02	<0.001
fish	56	6	2	11	1	30.29	<0.001
mammal	19	6	1	1	1	0.00	0.98
reptile	3	3	1	9	1	1.42	0.23
Invertebrate	123	1	1	16	1	114.13	<0.001
arachnid	1	0	0	0	–	–	–
clam	51	0	0	0	–	–	–
crustacean	3	0	1	5	1	2.76	0.10
insect	19	0	0	3	1	14.33	<0.001
snail	49	1	0	8	1	14.33	<0.001
Plant	346	3	37	83	1	273.69	<0.001
All recovery entities	587	29	44	133	1	415.28	<0.001

climatic adaptations may be particularly problematic for the recovery of species as climate changes. Therefore, recovery efforts aimed at maintaining the periphery of species ranges could be especially important. The differences between vertebrates and plants may also be an artifact of the way in which populations were defined by those writing listing documents and recovery plans.

Geographic Patterns of Decline

The general geographic patterns of declines in range and number of populations reflect in part the geographic clustering of taxonomic groups (Fig. 3). For example, populations of invertebrates have been extirpated throughout the United States, but there are more listed invertebrates in states east of the Mississippi River and south of New York. When all recovery entities are combined, declines of invertebrates offset the lower rates of decline of vertebrates in this region. Even within broad taxonomic groups, geographic patterns may be driven by the different numbers of certain taxa across regions. Range and population declines were more prevalent among vertebrates in the southwest, particularly in Arizona and New Mexico, than in other regions. These states have proportionally fewer endangered amphibians and reptiles, so the patterns are driven by declines of birds, mammals, and fishes (Fig. 1).

Within taxonomic groups, patterns of decline may be driven by geographic patterns of threats (Fig. 3). A lower proportion of plants in the western United States, especially the southwest, had range contractions and extirpations than plants in the east and in California. Threats in this region, such as water diversion and grazing by domestic livestock (Flather et al. 1998), are more likely to reduce habitat quality than cause habitat loss, perhaps limiting extirpations. Habitat loss and fragmentation due to land conversion, threats prevalent in the eastern United States and coastal areas (Flather et al. 1998), can be directly linked to extirpations and could also contribute to range contractions.

Patterns of range and population declines differed among islands under U.S. jurisdiction, areas often excluded in national-level assessments of threatened and endangered species (Fig. 3). Vertebrate and plant recovery entities on Pacific islands (Hawaii, Guam, and the Northern Marianas) had different patterns of range and population declines than those on Puerto Rico and the U.S. Virgin Islands. Ranges of most recovery entities in the former have been reduced and populations have been extirpated, whereas range reductions and extirpations have been recorded for half the recovery entities in the latter. Both these and the general geographic patterns we observed are derived from coarse-resolution geographic data. Species distribution data of finer resolution, especially for the invertebrates and plants that comprise 72% of the recovery entities with recovery plans, are not consistently or readily available in recovery plans.

Inference for Recovery Planning

The high percentage of recovery entities for which extirpations and reductions in overall abundance have been documented suggests that the common use of downlisting and delisting criteria expressed in terms of the number and size of populations (Wilcove et al. 1993; Tear et al. 1995; Gerber & Hatch 2002; M.C.N., unpublished data) is biologically warranted. Yet, despite the frequency of range contractions, recovery objectives rarely address range contractions directly. Quantitative downlisting or delisting recovery criteria have been set as the occupied proportion of the species' historic geographic range for 10 of the 1164 recovery entities (M.C.N., unpublished data). This mismatch may reflect the lack of quantitative data on range declines and land-use changes.

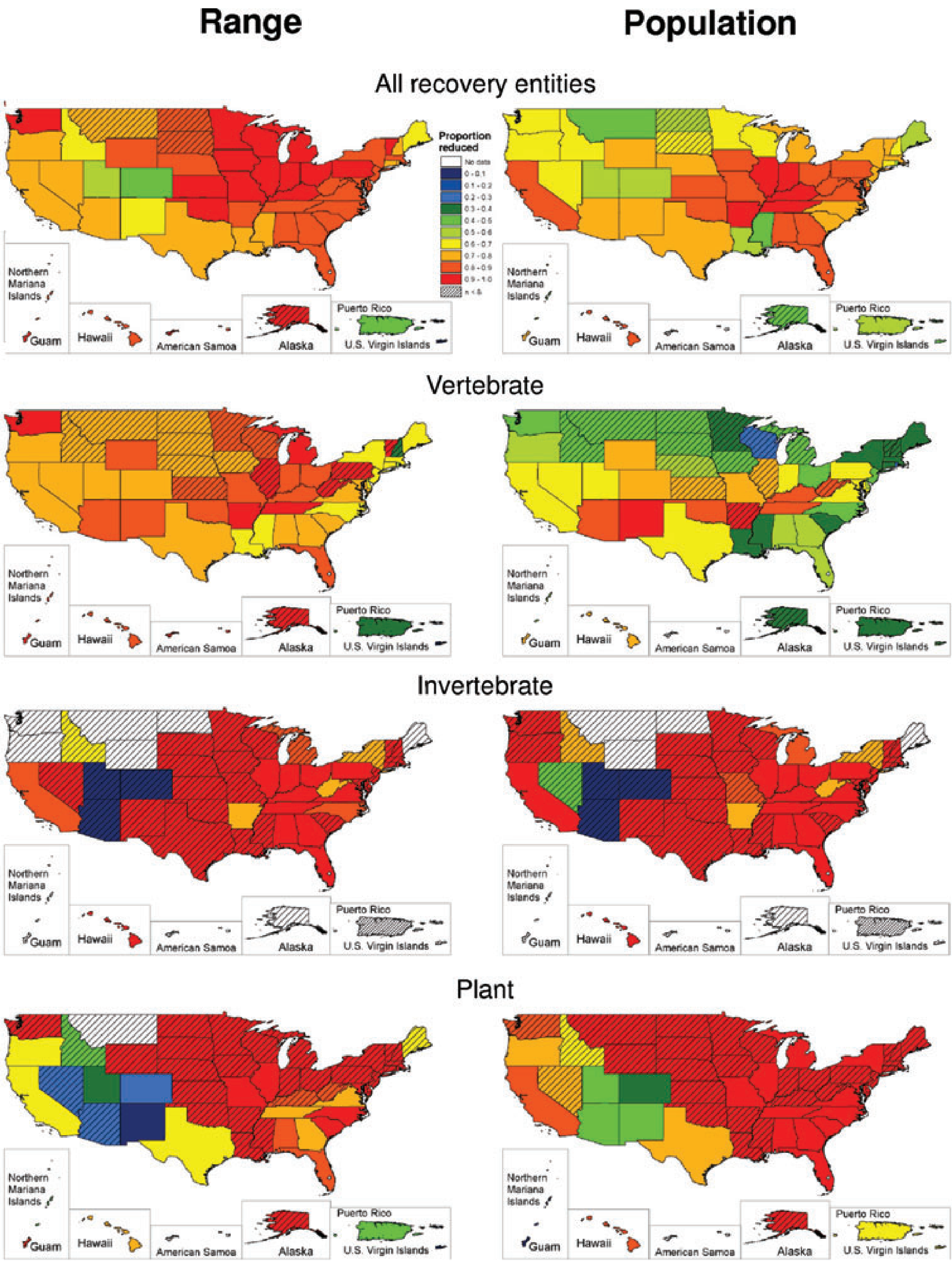

Figure 3. Geographic patterns of range contractions and population extirpations for all recovery entities (species, subspecies, and distinct population segments for which final recovery plans have been approved) analyzed and, separately, for 3 broad taxonomic groups. States or state equivalents (e.g., territory) for which the proportion was calculated with data from fewer than 8 recovery entities have hatch marks. Insets for islands and Alaska are at different scales from one another and from the continental United States.

Nevertheless, range is often incorporated qualitatively into recovery plans through recovery criteria that call for species to be maintained throughout their geographic distribution or stipulate that a certain number of populations be maintained in different geographic regions. Furthermore, for the 25 recovery entities that had range declines without extirpations (primarily vertebrates, Table 3), recovery criteria targeting increases in population size may indirectly promote range expansions. Nevertheless, a more direct quantitative criterion associated with range in recovery criteria might be useful for some species.

Conservation biologists frequently lament the lack of quantitative data for imperiled species that can be used to formulate recovery objectives and limited use of such data when they are available (Schemske et al. 1994; Tear et al. 1995; Schwartz 2008). Tear et al. (1995) found that recovery goals for approximately 90% of invertebrates required a specified number of populations for downlisting or delisting, although the number of populations was not known for 35% of species. Conversely, recovery goals for 40% of vertebrates were expressed in terms of the number of populations needed for recovery, although data on number of populations existed for 75% of vertebrates. It may appear that recovery criteria are being formulated without quantitative data and available quantitative data are being ignored. Our results, however, suggest that such a discrepancy may have a biological foundation. Most listed invertebrates had extirpations, so we think it is reasonable that recovery plans establish criteria related to the number of populations, even if historic or current data on the exact number of populations are not available. Fewer vertebrates had extirpations (Figs. 1 & 2), so we believe that the number of populations may not be the most appropriate objective to promote recovery even if the number of populations is known. If one wanted to compare quantitatively historic range size, number of populations, or abundance with those metrics at the time a recovery plan was written, data would be available for 4%, 49%, and 2% of recovery entities, respectively. Yet qualitative data for these same metrics were available for between 64% and 80% of recovery entities (Table 1).

Qualitative data on declines can focus recovery actions and priorities for future collection of quantitative data. For example, distances among some populations increase for species that have lost populations but still occupy the historical extent of their range. If research suggests these increased distances have affected dispersal and gene flow, recovery actions aimed at restoring connectivity may improve the species' status. In contrast, the status of species that have declined in range may be most improved by restoring the species to areas within its historic range in which habitat is still present and that extend the environmental gradients occupied by the species.

The association between the taxonomy and geography of threatened and endangered species and their pattern of decline met our expectations on the basis of broad traits of taxa and geographic variation of threats. Knowledge of these associations can help in the determination of recovery criteria. Ultimately, our results suggest that qualitative data can contribute substantially to informing species recovery efforts.

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