Broadening the Extinction Debate: Population Deletions and Additions in California and Western Australia

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Abstract: *Current discussions of biodiversity frequently center on the question of species extinction, and much of conservation biology focuses on this topic. We argue that species extinction often represents the endpoint of a process of population extinctions, and that the deletion of populations over much of a species' range is likely to be of as much or more concern than the final extinction of that species. Population extinctions often result from habitat destruction and modification, which can be widespread. The result is that species can be deleted from most of their former range but continue to persist in small refuge areas. Moreover, species additions in the form of invasive species are frequently more numerous than extinctions in any given area. Such invasions often result in dramatic changes in ecosystem structure or function and can be instrumental in hastening the extinction of native populations. We examine these premises using two examples from California and Western Australia. These two contrasting areas show broadly similar trends in species extinctions, range contractions, and invasions, and they illustrate the fact that, by concentrating on species extinctions, many of the important human effects on biodiversity can be overlooked.*

Ampliando el Debate sobre Extinción: Eliminación y Adición de Poblaciones en California y Australia del Oeste

Resumen: *Discusiones recientes sobre biodiversidad frecuentemente se centran en la extinción de las especies y una buena parte de la biología de la conservación se enfoca en este tema. Nosotros argumentamos que la extinción de especies representa frecuentemente el punto final de un proceso de extinciones de poblaciones y que la desaparición de poblaciones en la mayoría del rango de una especie es probablemente tanto o mas preocupante como la extinción final de las especies. Extinciones de poblaciones constantemente resultan de la destrucción y modificación del hábitat; lo cual puedo ocurrir con una extensión amplia. El resultado es que las especies pueden ser eliminadas de la mayoría de su rango original, pero continúan persistiendo en pequeñas áreas de refugio. Mas aún, la adición de especies en forma de especies invasivas son con frecuencia mas numerosas que las extinciones en un área determinada. Estas invasiones resultan frecuentemente en cambios dramáticos en la estructura of función del ecosistema y pueden ser el instrumento acelerador de la extinción de especies nativas. Examinamos estas premisas usando los ejemplos de California y Australia del Oeste. Estas dos contrastantes áreas muestran amplias tendencias similares en la extinción de especies, contracciones en rangos de distribución e invasiones. Además ilustran el hecho de que al enfocarnos en la extinción de especies muchos de los impactos humanos importantes en la biodiversiadad pueden ser desestimados.*

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Introduction

A central focus of conservation biology is the maintenance of biodiversity by preventing the extinction of species. Species extinction rates are reported to be increasing worldwide, and a large number of species are regarded as endangered (Pimm et al. 1995; United Nations Environment Program 1995). Although the focus on the deletion of species is understandable and necessary, it is also important to consider the overall dynamics of changing biodiversity. This includes not only the loss of species through extinction, but also the loss of populations through ecosystem modification and habitat loss and the gain of species via invasions.

We point out that the extent of species additions is, in fact, far greater than species losses, and that these additions can have significant effects on the ecosystems (and their component biota) they invade. Further, although extinction of species is the major focus for summary statistics relating to biodiversity, the extinction of populations through habitat loss and modification is a much more prevalent and pressing problem (Ehrlich & Daily 1993; Daily & Ehrlich 1995). The species level is one of several that need to be considered in a comprehensive approach to biodiversity conservation (Noss 1990; Noss & Cooperrider 1994). The focus on species extinctions is necessary because population extinctions may be reversible, but species extinctions generally are not. Moreover, species are frequently the focus of conservation legislation, as for instance in the U.S. Endangered Species Act (Kohm 1991). In many cases, however, species do not go extinct but are lost from a large part of their former range. Habitat loss and modification thus result in greatly reduced and/or fragmented populations. These dual topics of species additions and population—rather than species—extinctions deserve increased attention from conservation biologists and managers.

We examine these topics in detail for two different areas, California and Western Australia. These areas both contain a range of environments and climatic types, including extensive mediterranean-type and arid zones, but they are distant geographically and have different geologies, biotas, and histories of colonization and development (Hobbs et al. 1995*b*). The two areas thus provide contrasting cases with which to examine the question of species deletions and additions.

California

Species Losses and Gains

We reviewed the literature on a number of taxonomic groups to determine the total number of species present in California, the number extinct, those considered endangered by U.S. federal standards, as well as those of special concern to the California Department of Fish and Game. In addition, the number of known established invading species is listed. Included in this analysis are butterflies, amphibians, reptiles, birds, mammals, freshwater fish, and plants (Table 1). The resulting data show that, at the dates of each review, of 8274 total species in these categories 1109 were introduced (13.4%), 71 were endangered, and 49 were extinct (Fig. 1a). Numbers for endangered and extinct categories are inflated for a species count because they include subspecies categories.

Table 1. Californian and Western Australian biota that are native, introduced, threatened, or extinct.

Location species category	*Native*	*Introduced*	*Threatened*	*Extinct*
California[a]				
Plants	~6300	1023	30 (7 ssp)	34
Mammals	160	17	3 (2 ssp)	1
Birds	265	19	13 (6 ssp)	2 (both ssp)
Reptiles	76	3	1	0
Amphibians	45	2	2 (1 ssp)	0
Freshwater fishes	66	44	14	7
Butterflies	253	1	8 (all ssp)	5 (4 ssp)
Western Australia[b]				
Plants	12000+	1032	232	52
Mammals	141	17	30	11
Birds	510	10	36	0
Reptiles	750	0?	7	0
Amphibians	76	0?	2	0
Freshwater fishes	60	9	0	0

[a] *Data for California from Stebbins (1972), McGinnis (1984), Garth and Tilden (1986), Zeiner et al. (1988, 1990*a*, 1990*b*), Moyle and Williams (1990), Steinhart (1990), Vuilleumier (1991), Hickman (1993), and Skinner and Pavlik (1994). The threatened category does not include 857 species considered rare and endangered by the California Native Plant Association and 13 frogs, 13 reptiles, and 37 mammals of special concern to the California Department of Fish and Game. The extinct category does not include five mammal species extinct in California but extant elsewhere.*

[b] *Data for Western Australia from Serventy and Whittell (1976), Government of Western Australia (1992), and Keighery (1995). The threatened category does not include 1200 "priority flora" (species of uncertain conservation status that require further survey, research, and monitoring) and seven birds and four reptiles "in need of special protection."*

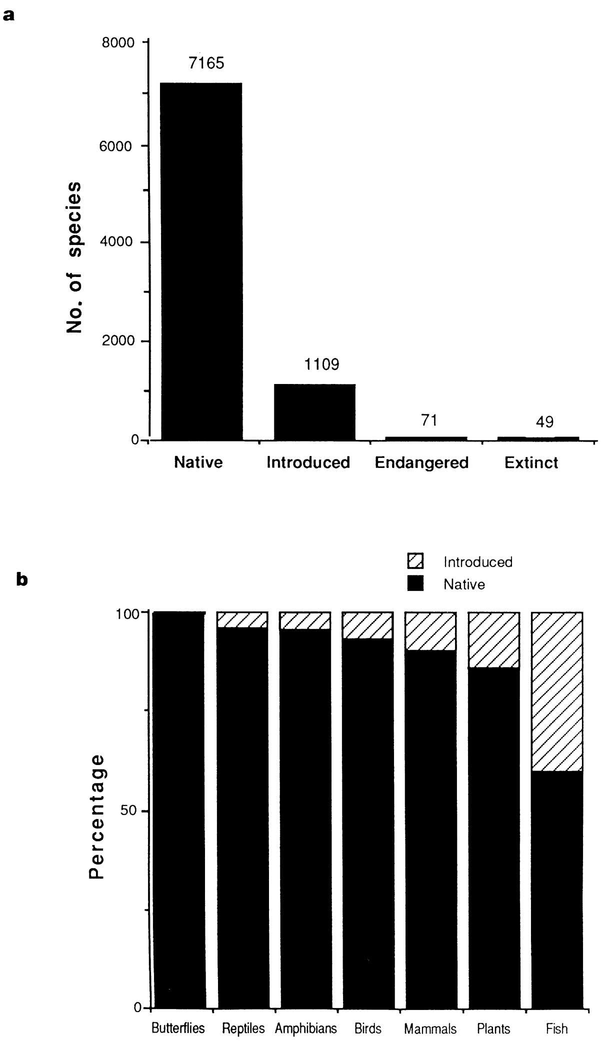

Figure 1. Number of Californian butterflies, reptiles, amphibians, birds, mammals, plants, and fish that are native, introduced, endangered, or extinct (a). Percentage of Californian biota that are native versus introduced species (b). Data and sources as in Table 1.

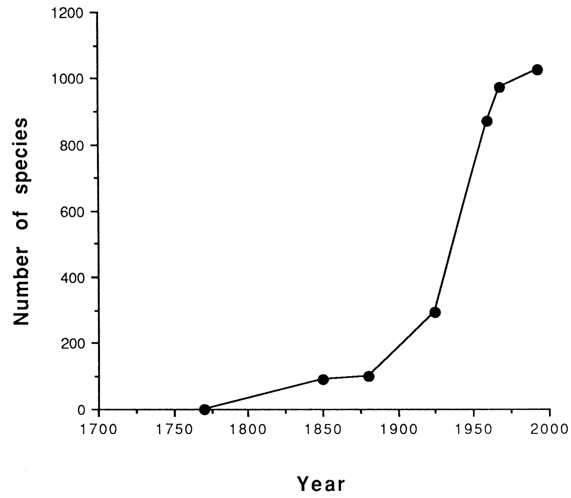

Figure 2. Numbers of nonnative plant species recorded in California over time, as estimated from accounts of the flora and other sources. Data from Rejmánek and Randall (1994).

Certain groups have been heavily affected by invading species, particularly freshwater fish and plants (Fig. 1b). Nearly half the freshwater fish species present were introduced, and Moyle (1996) points out that these nonnative species dominate many of the freshwater systems in California. Authorized and unauthorized introductions of fish into California have been documented since the 1870s, and, although no authorized introductions have been carried out since 1969, unauthorized introductions (either deliberate or accidental) have continued since then (Moyle 1976, 1996). Data on plant invasions collated from previous studies and inclusions in state Floras (Fig. 2) indicate that numbers of introduced plants increased exponentially since European colonization but may have slowed down recently (Rejmánek & Randall 1994). These authors also point out, however, that many species introduced in the past are now increasing in range and abundance.

Data on population extinctions are difficult to extract from the literature, but a number of examples are available for birds, amphibians, and freshwater fishes. A study by Soulé et al. (1988) documented the extinction of populations of birds from habitat patches following urban development and suggested that the process of habitat attrition and degradation, coupled with other factors such as predation from domestic cats, have resulted in the local extinction of a number of habitat-specific species.

For amphibians, the widespread decline of many species has been reported worldwide, and the suggested causes have been numerous (Hayes & Jennings 1986; Baringa 1990; Blaustein & Wake 1990; Blaustein & Wake 1995). There is ongoing debate as to whether human influences are primary causes for these declines or whether they reflect natural population variations (Pechmann & Wilbur 1994). In California numerous studies have documented extinctions of populations of frogs and other amphibians over extensive areas of their former ranges (Stebbins & Cohen 1995). Fellers and Drost (1993) report a study in which they resurveyed 16 historic localities and 34 other areas of suitable habitat of the Cascades frog (*Rana cascadae*) and found two frogs at only one site. They attributed the population extinctions at the other sites to a combination of factors, principally the introduction of nonnative predatory fish, drought, and habitat loss associated with management activities.

A series of studies has also documented extensive population extinctions of the mountain yellow-legged frog (*Rana muscosa*.). In a 1989 survey, Bradford et al. (1994), found frogs in only 1 of 27 sites in which they had been found 10 years previously. Other studies have found equivalent levels of extinction from former parts of the frog's range (Jennings et al. 1992; Stebbins & Cohen 1995). It is unclear what has caused this high level of population extinctions; a variety of explanations have been put forward, including drought, flood, pollution, and introduced fish (Stebbins & Cohen 1995). Bradford (1989) noted that frogs did not coexist with introduced fish in high Sierra Nevada lakes, and he later postulated that the fish effectively fragmented the frog habitat and prevented recolonization of sites where local extinction occurred (Bradford et al. 1993).

Further examples of extensive population extinctions are provided by the foothill yellow-legged frog (*Rana boylii*) and the red-legged frog (*Rana aurora*) (Hayes & Jennings 1988; Stebbins & Cohen 1995). Habitat destruction was suggested as a major cause of decline in both cases, and the impact of introduced species was considered important for *R. aurora*. Further population extinctions in these and other amphibian species are documented for the Yosemite area by Drost and Fellers (1996) and for the Central Valley by Fisher & Shaffer (1996). Both studies suggest that introduced species may be an important cause. A study of population extinctions of California newts (*Taricha torasa*) also suggested that introduced fish (*Gambusia affinis*) and crayfish (*Procambarus clarkii*) were the major agent causing local decline or extinction (Gamradt & Kats 1996).

Many examples exist of fish species that have very limited natural distributions and are rare for that reason (Minckley et al. 1991). But there are also examples in which distributions have been dramatically reduced by human activities. For instance, the Owens pupfish (*Cyprinodon radiosus*) was originally widespread in marshes and springs in the Owens Valley but declined dramatically in the first half of this century because of river channelization, water extraction, and the introduction of predatory game fish (Minckley et al. 1991). The species was thought to be extinct, but one population was rediscovered in 1956. The species has since been the subject of an intensive management program to increase population numbers and range, although introduced species continue to pose problems (Miller & Pister 1971; Minckley et al. 1991). Introduced species have also been implicated in range contractions and population extinctions of the desert pupfish (*Cyprinodon macularius*) (Schoenherr 1981). In the Salton Sea area, for instance, *C. macularius* has been replaced by introduced species such as the sailfin molly (*Poecilia latipinna*) and Zill's chichlid (*Tilapia zillii*) in all but a few localized habitats (Schoenherr 1981).

Habitat Losses

California has 4.1×10^5 km^2 of land and water surface. Of this, 11% is utilized for agriculture and another 4.4% represents urban, industrial, and road systems (Fay 1993). Noss and Peters (1995) find California ecosystems at extreme risk based on the number of endangered ecosystem types, numbers of endangered species, and the rate of development in the state. According to Noss and Peters, nearly half of the natural communities are rare or threatened. More specifically, Sawyer and Keeler-Wolf (1995) note that 135 of 280 recognized vegetation types are rare enough to warrant special protection, and at least 50 have less than 900 ha of high quality habitat. It is not clear, however, how many of these communities were naturally rare or limited in extent.

Data on the loss of California's habitats through time do not exist in precise form, but the numbers that do exist are dramatic. Jones and Stokes, Associates (1987), and Lekisch (1991) give comparable values for loss of habitats of major biomes since the early 1800s. These are 80%, 66%, and 89% loss of coastal wetlands, vernal pools, and riparian woodlands, respectively. Loss estimates for interior wetlands are 94% and 96%, respectively, by these sources. The total area of wetlands in California is estimated to have declined from 1.9-2.3 million ha in 1850 to about 136,000 ha in 1980 (Smith 1993). Lekisch (1991) gives a figure of 99% loss for the valley grassland that covered much of the Central Valley and that was transformed by stock grazing, introduced annual plants, and cultivation (Huenneke & Mooney 1989; Heady et al. 1992; Barbour et al. 1993). In addition, riparian forests in the Central Valley are estimated to have declined from over 419,000 ha last century to 46,000 ha (11%) in 1980 (Katibah 1984). In 1985 only 136,000 ha of virgin redwood forest was left of the original 909,000 ha. Westman (1981) also reports that 85–90% of the coastal sage community has been lost.

These numbers give a sense of the loss of some key ecosystem types but do not indicate the generalized degradation of ecosystems due to fragmentation and direct and indirect anthropogenic impact. Data collated by Jensen et al. (1993) indicate that extensive ecosystem conversion to agriculture and urban development is continuing, with, for instance, 1.4 million ha of grassland and 260,000 ha of valley foothill woodland being converted between 1950 and 1980. The task of documenting habitat change in California is an important one and needs to be undertaken, even though the job will not be easy because of the great number of habitat types and the variety of disturbances to them.

Western Australia

Species Losses and Gains

Western Australia covers 2.53×10^6 km^2, or about one-third of the continent of Australia. It contains approximately half of the described plant species for the continent, and the southwest botanical province (0.3×10^6

km^2) is a recognized hotspot for floristic biodiversity (Groombridge 1992; Hopper et al. 1996). This area also has the highest concentrations of declared rare flora in Australia (this includes a variety of designations of endangerment). Out of a total of around 12,000 species, 52 are thought to have gone extinct, 232 are considered threatened, and a further 1200 are of uncertain status because of a lack of information. Greuter (1994) has estimated that Western Australia has the highest rates of plant extinction and endangerment of all the areas with mediterranean climates. The flora is still under active research, and estimates of total species numbers are approximate. By current estimates, approximately 8.6% of the total flora is introduced, a figure that is lower than for Australia as a whole. Over all the biotic groups considered here, 7.3% of the total number of species are introduced, a figure markedly lower than that for California. The overall pattern of numbers of species in each category is remarkably similar to that for California (Fig. 3a), although there is a higher percentage of introduced mammals and a lower percentage of introduced species in other groups in Western Australia (Fig. 3b).

Recent estimates indicate that plant introductions into Western Australia continue, with numbers of naturalized taxa increasing from 848 in 1985 (Green 1985; Keighery 1991) to 1032 in 1995 (Keighery 1995), and there are recent examples of introduced species rapidly extending their ranges (Dodd & Moore 1993). Introductions of other groups also continue; Hutchison and Armstrong (1993) detail the history of the recent invasion of a Western Australian river system by the fish *Perca fluviatillis.*

No extinctions have been recorded for Western Australian birds, reptiles, amphibians, or freshwater fishes. Australia has one of the highest extinction rates for mammals in the world, however, and the extinction rate masks the more widespread problem of range contractions (Strahan 1983; Burbidge & McKenzie 1989; Kennedy 1990). Mammals that were formerly widely distributed across the continent are now restricted to small refugia or offshore islands. Twenty-one percent of the remaining mammal species are considered threatened. Twenty-six species now occur only as remnant populations occupying less than 20% of their former range (Short & Smith 1994). It follows from this that many populations of these mammals have gone extinct across the continent. Data from Kitchener et al. (1980) show the contrast in extinction rate within a particular region, compared with the overall rate (Fig. 4). Of mammal species originally found in the wheatbelt region 42% are now extinct there, whereas only 14% of the same species are extinct over the whole state. There is increasing evidence that these population extinctions may have had system-level repercussions, for instance by removing the influence of soil disturbance and browsing by marsupials (Noble 1993). But, it is difficult to assess these effects accurately due to lack of baseline data.

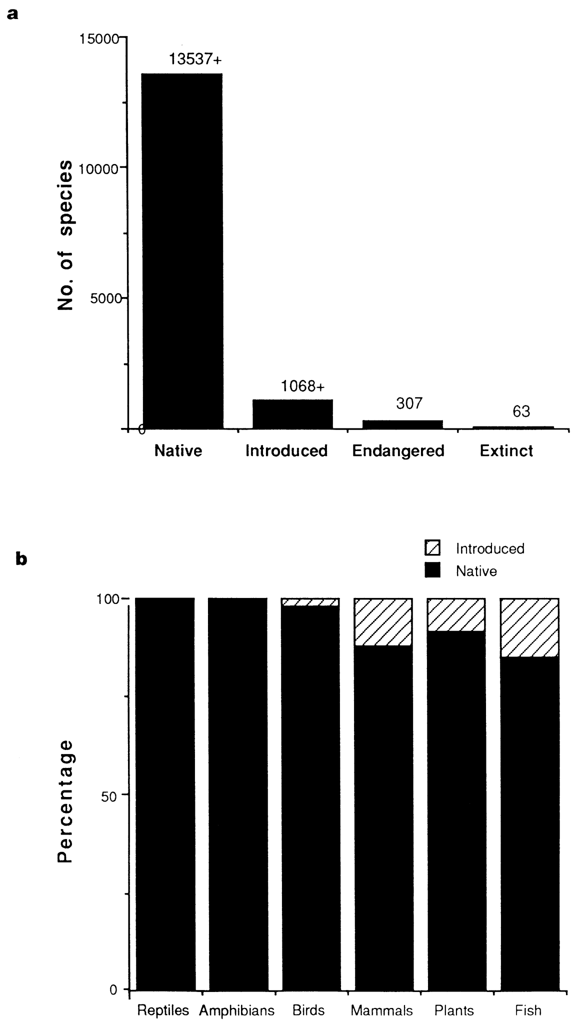

Figure 3. Number of Western Australian reptiles, amphibians, birds, mammals, plants, and freshwater fish that are native, introduced, endangered, or extinct. (a). Percentage of Western Australian biota that are native versus introduced species (b). Data and sources as in Table 1.

Despite there being no species extinctions recorded for the other faunal groups, evidence for birds suggests significant range contractions for many species. Over half the bird species recorded from the agricultural area in the southwest of the state have declined in distribution or abundance since the start of this century (Saunders & Ingram 1995). This has resulted in population extinctions at local and regional scales (Saunders 1989, 1990, 1993). These declines are evident for the majority of species whose primary habitat is native vegetation, whereas species that have increased in abundance are those associated with towns and agriculture (Fig. 5). A striking illustration of the process of population extinction is the decline in range of the Carnaby's cockatoo

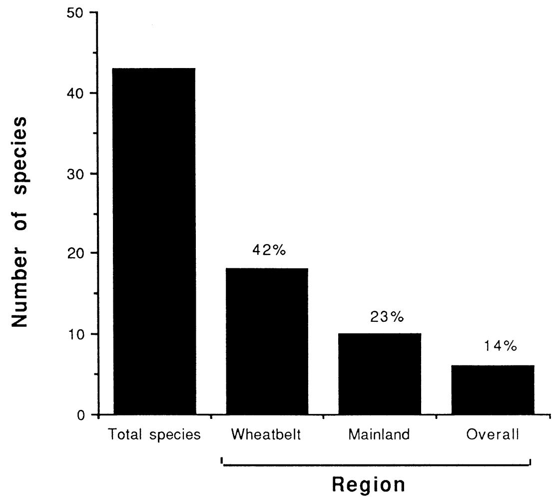

Figure 4. Numbers of mammal species originally recorded from the wheatbelt region of Western Australia, and the numbers of these species now extinct in the wheatbelt, extinct on mainland Western Australia but still present on offshore islands, and extinct overall (i.e., on mainland and offshore islands). Data from Kitchener et al. (1980).

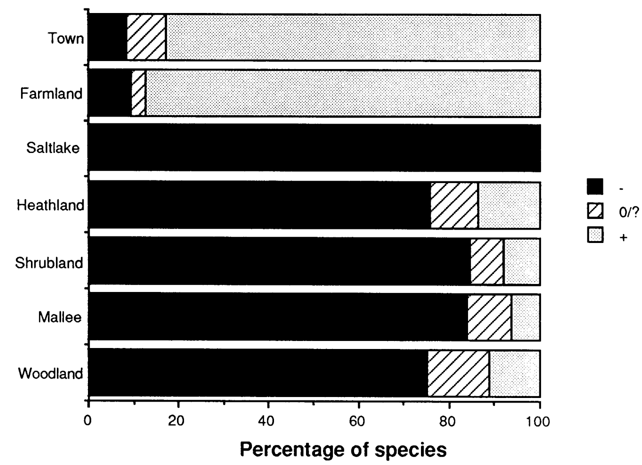

Figure 5. Changes in range and/or abundance of resident passerines, categorized by habitat, in the wheatbelt of Western Australia between the periods 1900–1937 and 1987–1990, as estimated from historical records and volunteer recordings: decline in range and/or abundance (−), no change or insufficient data to assess change (D/?), increase in range and/or abundance (+). Data from Saunders and Ingram (1995).

(*Calyptorhynchus funereus latirostrus*; Saunders 1990; Saunders & Ingram 1995). In 1968 the species was recorded by 100% of observers distributed throughout the 14 million ha of the wheatbelt area, but by 1987 this had declined to 31% of observers. Birds were found only around the fringes of the agricultural area, where significant amounts of adjacent native vegetation remained.

Habitat Losses

Large areas of Western Australia are arid or semiarid and hence have been relatively little modified since European settlement. Most settlement occurs on the coast, with the largest population densities in the southwestern corner. The most significant impact over much of Western Australia has been that of pastoralism, and a high proportion of pastoral land is considered degraded in some way (Hobbs & Hopkins 1990). Thus, habitat modification rather than loss is the main concern for much of the state.

The southwestern portion of the state is that most heavily modified by human activities, and agriculture and urbanization have resulted in significant reductions in the area of many ecosystem types. The 1.56×10^5 km^2 of land that has been cleared for agricultural production in this area has resulted in significant reductions in many vegetation types (Saunders & Hobbs 1992). Of the 44 vegetation types recognized in the area, many have been significantly reduced in extent, predominantly because of agricultural development (Table 2; Fig. 6; Beard & Sprenger 1984; Hobbs et al. 1995*a*), and 9 inhabit less than 10% of their original extent. Two restricted types are believed to have been almost completely eliminated. In addition to habitat loss due to clearing, many vegetation types are threatened by degradation of various sorts, including land clearing, secondary salinization, and introduced disease.

Discussion

Although species extinction is the focus of much conservation activity and debate, we suggest that the addition and deletion of populations over large parts of the Earth, often in conjunction with massive losses of habitat, are of equal concern. The process of species extinction is often simply the endpoint of a process of population extinctions throughout the former range of a species. At the same time that native species populations are being driven to extinction, populations of other native and nonnative species are increasing. This represents a dual threat, not only to biodiversity but also to the conservation and production values of many ecosystems. Data on species extinctions are relatively easily accessible, but data on population extinctions are difficult to assemble (Ehrlich 1994). The same is also true of the increase in numbers of populations of all but a few invading species. We believe that serious efforts need to be taken to redress this lack of information and concomitant lack of concern.

Table 2. Vegetation units of southwestern Australia, showing their total original area, their percentage contribution to the area of the province, and the percentage of each unit that has been cleared.*

Unit no.	*Physiognomic unit*	*Floristic*	*Area km²*	*Percentage of total*	*Cleared (%)*
1	tall forest	*E.diversicolor, E.marginata, E.calophylla*	4004	1.29	14
2	tall woodland	*Eucalyptus gomphocephala*	69	0.02	94
3	forest	*Eucalyptus marginata*	31802	10.26	44
4	woodland	*Eucalyptus calophylla–E.wandoo*	16697	5.39	94
5	woodland	*Eucalyptus astringens–E.accedens*	958	0.31	72
6	woodland	*Eucalyptus gomphocephala* ± *E.marginata*	1039	0.34	90
7	woodland	*E.loxophleba, E.salmonophloia, E.wandoo*	41126	13.27	97
8	woodland	*Eucalyptus salmonophloia–E.salubris*	17580	5.67	78
9	woodland	*E.le souefii–E.transcontinentalis–E.oleosa*	950	0.31	0
10	woodland	*Eucalyptus oleosa–E.flocktoniae*	1575	0.51	0
13	open woodland	mainly *Eucalyptus wandoo*	221	0.07	94
14	low forest	*Eucalyptus marginata*	964	0.31	82
15	low forest	*Callitris preissii*	29	0.01	100
16	low forest	*E.platypus* or *E.cornuta–E.lehmannii*	113	0.04	2
17	low forest	*Acacia rostellifera*	327	0.10	98
22	low woodland	*Agonis flexuosa*	242	0.08	74
23	low woodland	*Banksia* spp., ± *Eucalyptus marginata*	6229	2.01	61
25	low woodland	*Allocasuarina huegeliana–Eucalyptus loxophleba*	88	0.03	88
26	low woodland	*Eucalyptus marginata–Allocasuarina fraserana*	901	0.29	41
27	low woodland	*Melaleuca* spp.	926	0.30	49
30	low woodland and scattered emergent trees	*Banksia* spp. + *Eucalyptus marginata*	680	0.22	100
31	thicket with low woodland and scattered emergent trees	*Allocasuarina campestris* + *E.wandoo* or *Melaleuca uncinata* + *E.loxophleba*	441	0.14	98
35	scrub and scattered trees	*Acacia* spp. + *Eucalyptus* and/or *Callitris*	5354	1.73	83
36	thicket	*Acacia-Allocasuarina-Melaleuca*	35496	11.46	80
37	thicket	*Melaleuca rhaphiophylla*	143	0.05	74
38	thicket	*Dryandra* spp. and/or *Eucalyptus* spp.	497	0.16	18
40	scrub	*Acacia* spp.	1109	0.36	78
41	scrub	*Melaleuca* spp.	76	0.02	70
42	scrub	*Agonis flexuosa, Acacia, Eucalyptus*	1636	0.53	12
44	sparse scrub	*Acacia* spp.	121	0.04	66
45	mallee	*Eucalyptus* spp.	46385	14.97	55
131	mallee and woodland patches	*Eucalyptus* spp.	22219	7.17	40
47	mallee-heath	*E.tetragona* + mixed Proteaceae-Myrtaceae	17114	5.52	69
47a	tree heath	Heterogeneous	3626	1.17	0
48	scrub heath	Heterogeneous, Proteaceae-Myrtaceae	35070	11.32	61
49	heath	Heterogeneous, Proteaceae-Myrtaceae	2554	0.82	41
51	sedgeland	Cyperaceae, Restionaceae	449	0.16	48
119	succulent steppe, thickly wooded	*Atriplex, Maireana* + *Eucalyptus* spp.	4486	1.44	87
121	succulent steppe, lightly wooded	*Atriplex, Maireana* + *Acacia* spp.	104	0.03	68
124	succulent steppe, unwooded	Samphire: *Halosarcia*	313	0.10	64
125	bare areas, playa lakes		4896	1.58	30
126	bare areas, freshwater lakes		123	0.04	54
128	bare areas, rock outcrops		413	0.13	54
129	bare areas, drift sand		645	0.21	10
44 Units		Total	309840	100	65
				12.3% of state	

**From Hobbs et al. (1995*b*), adapted from Beard and Sprenger (1984).*

Extinctions

One result of the focus on species extinction by conservation organizations and environmentalists has been the questioning of the validity of that focus by those who argue that current environmental concerns are unfounded. We do not have a clear picture of the number of species present on Earth, and in many cases we do not know current rates of extinction or have scant evidence to support suggested rates (May 1988; Heywood & Stuart 1992; Reid 1992; Smith et al. 1993). In Western Australia, for instance, botanical exploration and taxonomic work have resulted in a large increase in the number of described plant species recognized over the past 30 years, and several species presumed extinct have since

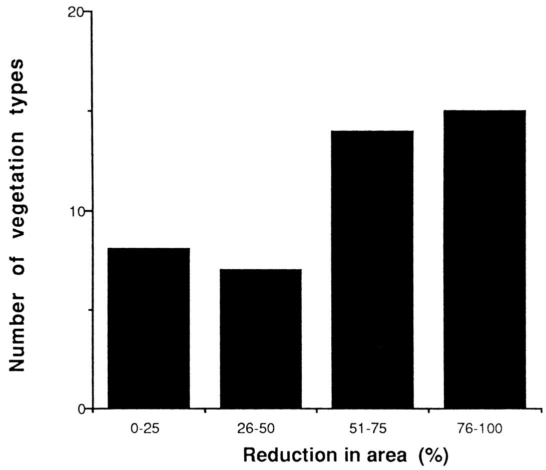

*Figure 6. Reduction in area of vegetation types in southwestern Australia, expressed as the number of vegetation types experiencing different degrees of reduction from the original extent. Data from Beard and Sprenger (1984); see also Hobbs et al. (1995*a*).*

been rediscovered (Hopper et al. 1990; Hopper 1992). In addition, published accounts differ dramatically in their allocation of species to different categories (Mace 1994). For instance, estimates of threatened plant species range from 30 to 887 for California and from 232 to 1432 for Western Australia, depending on which reference is cited or which categories of endangerment are included.

Given this degree of uncertainty and taxonomic fluidity, and the additional fact that many species are naturally rare, it can be argued that the current concern over species extinction is unfounded (Mann 1991). This argument is then used to criticize current thinking on the need for conservation measures, especially where these are expensive and run contrary to other societal objectives (Easterbrook 1995; Simon & Wildavsky 1995).

This line of reasoning successfully ignores the bigger picture of species extinctions, however, as highlighted here: namely, that species extinction is simply the endpoint of a process of population extinctions. This is not a new message (Shaffer 1981; Gilpin & Soulé 1986; Ehrlich & Daily 1993; Caughley 1994) but one that bears repeating because of its significance. Moyle and Williams (1990) illustrate the problem in relation to the fishes of California. Twelve percent of the native taxa are considered threatened or endangered, and only 36% are considered secure; the remaining taxa have declining populations but are not considered endangered yet. To be listed as endangered, a species must already have extremely low numbers. The process of population extinction is intimately related to habitat loss (Ehrlich 1994), and Hughes et al. (unpublished data) suggest that the relationship between the two is linear. Because we often have little information on population extinctions, habitat loss could be used as a surrogate measure. From the data presented here, population extinction is therefore a widespread phenomenon in both the regions studied and most likely in many other parts of the world (Hughes et al. unpublished data).

Local population extinctions form part of normal metapopulation dynamics driven by demographic and environmental stochasticity (Hanski & Simberloff 1997). For instance, the bay checkerspot butterfly, (*Euphydryas editha bayensis*) is thought to exhibit metapopulation dynamics in the San Francisco Bay area, with a core population on a large area of habitat and numerous smaller populations in the surrounding district (Harrison et al. 1988; McGarrahan 1997; Thomas & Hanski 1997). As habitat decline and land-use change continue, however, opportunities for reestablishment of local populations that go extinct become increasingly scarce. In addition, extinction of components of the metapopulation may have significant effects on its dynamics (Murphy et al. 1990; Harrison 1994). Recent analyses suggest that metapopulations may exhibit nonlinear dynamics and collapse to extinction even with only small habitat changes (Hanski et al. 1995).

Population extinctions may have important consequences, especially where marked genetic variation exists between populations or where populations form part of a larger metapopulation. There is increasing evidence for the existence of complex patterns of genetic variation among different populations of the same species. For instance, plants such as *Isotoma petraea* and *Stylidium crossocephalum* in Western Australia have been found to exhibit marked genetic variation across their ranges (Coates & James 1979; James 1982; Lavery & James 1986; Hopper 1992). Ehrlich (1992) has also summarized evidence suggesting that different populations of the checkerspot butterfly (*Euphydryas editha*) in California differ in genotypes, phenotypes, phenologies, resource use, and behavior. The retention of a few populations will not, in that case, ensure the persistence of the range of variation found in the species.

In addition to these considerations, loss of local populations means the loss of the functional role of these species. This may be particularly important where the species are keystones or "ecosystem engineers" (Mills et al. 1993; Jones et al. 1994; Stone 1995). Extinctions of populations of economically important species can also have important direct economic and social effects. For instance, Lackey (1996) has recently pointed out that many stocks (roughly equivalent to populations) of Pacific salmon have declined or become extinct, even though no species of salmon as a whole is threatened.

We need therefore to expand the focus of our efforts from preserving endangered species to include preventing the endangerment in the first place. A major focus of concern should be on the ecosystem modification and population declines that have resulted in species endangerment, rather than simply on the plight of the remaining populations. This is not to suggest that efforts to save species from extinction should be reduced. But, if we focus on preserving a select group of species in danger of extinction and shy away from dealing with the broader issues of system decline leading to the endangerment of those species, we will end up with many more problems and endangered species to deal with.

A recent analysis of the plant communities of southwestern Australia identified the main processes threatening a range of communities thought to be in imminent danger of major structural and floristic change (Government of Western Australia 1992). The most frequently cited threats were land clearing, secondary salinization, and introduced disease. These processes are also important threats to many of the species currently listed as endangered. Tilman et al. (1994) have discussed the destruction of habitat in terms of creating an "extinction debt," a concept that essentially revisits the idea of species "relaxation" (MacArthur & Wilson 1967; Diamond 1975). By reducing available habitat and driving populations to extinction, land clearing, fragmentation, and degradation are producing a legacy of species that no longer retain populations that are viable in the long term and that are therefore doomed to extinction. These same processes are significantly affecting large areas of production and conservation lands in southwestern Australia (Hobbs et al. 1993; Withers et al. 1994; George et al. 1995). The processes leading to endangerment and extinction are hence also leading to declining agricultural and forestry production. A broader perspective of the species extinction problem thus makes it evident that species extinction is only one of a suite of consequences of human use and modification of the earth's ecosystems.

Species Additions

Biotic invasions are ongoing worldwide, the full extent of which has yet to be fully documented (Drake et al. 1989; U.S. Congress 1993). Nevertheless, invasions have become recognized as a major factor forcing global environmental change (Vitousek et al. 1996). The relatively high levels of invasion by mammals, plants, and fish in both California and Western Australia undoubtedly result mainly from the deliberate introduction of these organisms for agriculture, horticulture, or sport. In both areas, recent indications suggest that relatively large numbers of new species of plants continue to be introduced (Rejmánek & Randall 1994; Keighery 1995). There is still considerable potential for inadvertent introduction of nonnative species in other groups—for instance, as contaminants of agricultural produce, in ballast water, or in other forms of transport (Carlton & Geller 1993; Hedgpeth 1993).

Some commentators suggest that we should not be concerned about species introductions because they serve to increase the species diversity of an area (e.g., Simon & Wildavsky 1995). This argument essentially ignores both the value of retaining indigenous biotas across the globe and the potential for invading species to have deleterious effects on native species and on the conservation or production values of ecosystems. We have given several examples of the interaction between invasion by nonnative species and the population extinction of native species. Invasions by individual species also have the capacity to have major effects on the systems invaded. In tropical and arid Australia, plant invasions lead to dramatic changes in ecosystem structure and function (Braithwaite et al. 1989; Griffin et al. 1989; Humphries et al. 1991; Humphries 1993). In southwestern Australia, combined invasions by nonnative annual plants lead to reduced regeneration of native species and changed fire regimes (Hobbs & Atkins 1991). Invasions in California also alter fuel loads and structures and hence affect fire regimes (Robles & Chapin 1995), a common result of invasions—especially by grass species—in many parts of the world (D'Antonio & Vitousek 1992).

It could also be argued that, given the large numbers of introduced plant species in both California and Western Australia, relatively few species actually cause any major problems. But those few species are capable of causing widespread ecosystem disruption and economic loss. In addition, there is the potential for many more species to become problems as they move from a "lag phase" of relatively limited spread to a phase of exponential population expansion (Hobbs 1993; Hobbs & Humphries 1995; Crooks & Soulé 1996).

Invasions by foxes and feral cats have also had dramatic effects on the native fauna of Australia, to the extent that many once-widespread species are now either extinct or restricted to small fractions of their original range (Kinnear et al. 1988; Friend 1990; Hobbs et al. 1993). In addition to introduced species, native species extending their range can also have significant impacts. For instance, the galah (*Cacatua roseicapella*), which has invaded the Western Australian agricultural area from the arid zone, is implicated in woodland decline because of its habit of ringbarking trees, and it competes with native species such as Carnaby's cockatoo (Saunders 1990; Saunders & Ingram 1995).

These examples further illustrate the potential for invasions to enhance the extinction or endangerment process. We have not considered insect and disease organisms here, although these groups constitute a major threat to natural and production systems (Campbell & Schlarbaum 1994; Withers et al. 1994).

Conclusion

Unfortunately, given the current state of our knowledge and the complexity of natural systems, it is usually difficult to predict the impact of any given addition or deletion of a species. Current rates of development and land-use change inevitably lead to increased deletion of populations, regardless of whether or not the species as a whole goes extinct. Habitat destruction and transformation are important ongoing processes leading to population deletions in both the areas we examined, and we argue that these areas are representative of many parts of the earth. Deletion of native populations and addition of nonnatives may have unexpected and long-term ecological consequences. Does it matter? In the end, human society is faced with the prospect of (1) the majority of the species native to a region being reduced to a few populations sequestered into increasingly small refuges and (2) the remainder of the area being dominated by human activity and an increasingly homogeneous set of introduced species. More open and rational debate on the desirability and sustainability of such an outcome is urgently required.

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