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CHANGES IN SPECIES ASSEMBLAGES WITHIN THE ADELAIDE METROPOLITAN AREA, AUSTRALIA, 1836–2002

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Abstract. Currently, slightly less than half the world's population lives in dense urban areas, principally cities. In Australia, nearly 85% of people live in towns with 1000 or more residents. Although individual species of urban flora and fauna have often been well studied, little is known of the long-term temporal patterns associated with changes in both the abiotic and biotic environments as urban systems expand. Using historical and current information, the changes in species richness (defined as the native and introduced vertebrates and vascular plants) in Adelaide, South Australia, are described from its founding in 1836 until 2002. Adelaide is an isolated city of over a million inhabitants, bordered by a range of hills and the South Australian coastline. With a Mediterranean climate, a culture that places high importance on private residential gardens, and the presence of extensive public parklands, the metropolitan area has a significant diversity of both native and introduced flora and fauna. Using only the presence or absence of a species, the changes to plant and vertebrate species richness were quantified by analyzing the observed patterns of change at a functional group level. Powerful correlative evidence is provided to explain the development and establishment of patterns in urban ecology.

There has been a dramatic change in species composition, with an increase in total species numbers of ~30%. At least 132 native species of plants and animals have become locally extinct, and a minimum of 648 introduced species have arrived (mostly plants). The plants increased in species richness by 46%. Fifty percent of the native mammal species were lost, and overall, the birds declined by one species, representing 21 extinctions and 20 successful introductions. Amphibians and reptiles showed no net change. The herbaceous perennial and annual plant species richness showed a substantial increase. This temporal approach to urban ecology demonstrates new ways to identify individual species or groups at risk of extinction and provides some long-term management goals for large urban areas.

Key words: amphibians; anthropogenic; birds; graphical analysis; historical; mammals; plants; reptiles; South Australia; species richness; urban ecology.

INTRODUCTION

Urban ecosystems have been defined as areas ''in which people live at high densities (equal to or greater than 186 people/km^2), or where the built infrastructure covers a large proportion of the land surface'' (Pickett et al. 2001). The United Nations suggests that the world will have 61% of its population living in urban areas by the year 2030 (United Nations Population Division 2004). Moreover, the development of urban environments is a principal cause of land use change worldwide (Miller and Hobbs 2002). The situation in Australia is particularly significant, as nearly 85% of Australians live in towns with 1000 or more inhabitants (Aplin 1998).

The vast majority of ecological studies have focused on rural, agricultural, and natural environments, with little emphasis on urban areas. There has generally been poor documentation of the assemblages of urban flora and fauna (Niemelä 1999), but where comprehensive surveys have been undertaken, the species diversity (an index of community diversity that takes into account both species richness and the relative abundances of species; Begon et al. 1996) is often found to be remarkably high (Miller and Hobbs 2002). Urban systems contain assemblages of flora and fauna that are a direct result of human influence (Niemelä 1999). Although cities generally have a greater ratio of introduced to native species than natural areas (Kloor 1999), urban areas can contain a high diversity of native species.

Urban ecology originally developed in Europe during and after World War II (e.g., studies of vegetation in urban bombsites; Salisbury 1943). Since then, there have been numerous studies on the structure and composition of urban vegetation (such as Stalter et al. 1996), many of which are long term (e.g., Kent et al. 1999, Maurer et al. 2000, Godefroid 2001, Chocholouskova and Pysek 2003). Typically, however, the data primarily consist of species lists for the city and occasionally maps of the distribution of individual species across the urban area (e.g., Kowarik 1990). There is a lack of general urban temporal studies, and there are also very few that have taken a systematic approach to species–area data through time (Kent et al. 1999).

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At present, the dominant land use for the Adelaide area is cropping and pasture (slightly greater than two-fifths), closely followed by urban habitats (slightly less than 2/5ths), while the remaining one-fifth is composed of remnant vegetation, orchards, irrigated areas, water bodies, quarries, swamp, hardwood plantations, and pine plantations (Oke 1997). Most Adelaide residences have front and back yards, and there are extensive parkland regions that either contain remnant natural bushland or are highly modified. Adelaide is a good model for this type of historical study due to the fact that the municipal boundaries have not changed, thus reducing error from the use of multiple checklists.

Historically, the Adelaide region has supported a diverse range of natural habitats. Before its founding, the Adelaide plains supported ~1130 vascular plant species, ~285 native bird species (including migratory and nomadic species), 40 mammal species, 52 reptile species, and 7 amphibian species (Kraehenbuehl 1996, Turner 2001). Adelaide can be used as an effective model for historical and ecological studies because excellent data on both the plants and animals of Adelaide have been regularly and systematically collected since 1836.

The vegetation throughout the region has been heavily cleared (with disproportionate clearance of temperate woodlands; Paton et al. 2000). The larger patches of remnant vegetation are situated within the >10 000 ha of Adelaide's national, conservation, and recreation parks. Other naturally growing plants are now present in vacant blocks, roadside verges, ponds, along rivers, railway embankments, and suburban parks. Less than 4% of the natural vegetation now remains on the Adelaide plains (Oke 1997).

The changes in Adelaide's biotic diversity from its founding to the present day are described here. The first goal was to test three primary hypotheses. Firstly, that total plant and animal species numbers have increased since the founding of Adelaide in 1836. It is argued that with the increase in worldwide, intra- and interstate travel, and the escape and spread of introduced garden plants, there has been an increase in species richness (particularly plant species) greater than the potential extinction of native species.

Secondly, total species numbers of introduced plants/vertebrates within the Adelaide region have increased since the founding of Adelaide, but this increase is slowing. There are recent reports indicating a renewed interest in preventing the introduction and spread of exotic species through public education and awareness (Parker 2001), early detection and treatment of invasions before spread occurs (Hobbs and Humphries 1995), and finding new methods to determine a species' invasibility potential (Parker 2001).

Thirdly, it is hypothesized that total species numbers of native plants/vertebrates within the Adelaide region have decreased since the founding of Adelaide, but this decrease is slowing. This hypothesis follows from the observation that, as the species more susceptible to urbanization, agriculture, and grazing practices are lost, leaving the hardier species to remain in the habitat for longer, the rate of species loss will gradually decrease. Also, as Adelaide has expanded, there has been more of an effort (driven by both the general public and local and state governments) to preserve and promote the establishment and survival of native species.

A second goal was to explain the patterns produced through changes in species compositions, by analyzing these patterns at a functional group level.

Methods

Study site

The Adelaide metropolitan region is situated on the southeastern side of Gulf St. Vincent, within the state of South Australia, Australia. As defined in the South Australian Development Act 1993, the Adelaide metropolitan region spans an 80-km north–south axis covering >185 000 ha from Sellicks Beach in the south to Gawler River in the north, and is bound by the southern ocean and Gulf St. Vincent in the west and the escarpment of the Mt. Lofty Ranges in the east and south (Fig. 1). Adelaide is characterized by a Mediterranean climate and is the driest Australian capital city, with an average rainfall of 585 mm per annum between 1977 and 1997 (Crittenden 1999). The wettest months are from May to August. The summers are hot and dry (average maximum is 28°C), and the winters are reasonably mild with a mean maximum temperature of 16°C. The soils are primarily podzolic in the hills area, changing to red brown sandy clay/earth/clay loam soils within the lower-lying plains area (Warburton 1977).

Adelaide was founded on 28 December 1836 as an independent English colony. Adelaide currently has a population of ~1.1 million people (Australian Bureau of Statistics 1999). It is thought that Adelaide had the richest source of biodiversity in South Australia before European settlement, possibly a consequence of the substantial variation in topography, geology, rainfall, and microclimate (Oke 1997). The region includes a wide range of vegetation types.

Database

Species richness (the number of species present in a community; Begon et al. 1996), as opposed to species diversity, was chosen as the most reliable method for gaining useful historical information from a temporal analysis of Adelaide's biota. A database was created from historical and current information on the species present in Adelaide, and the years in which they were located within this region between 1836 and 2002. No attempt was made to collect data on species abundances, because of the lack of accurate historical records.

The species of plants and animals (both native and introduced) currently found within the Adelaide region

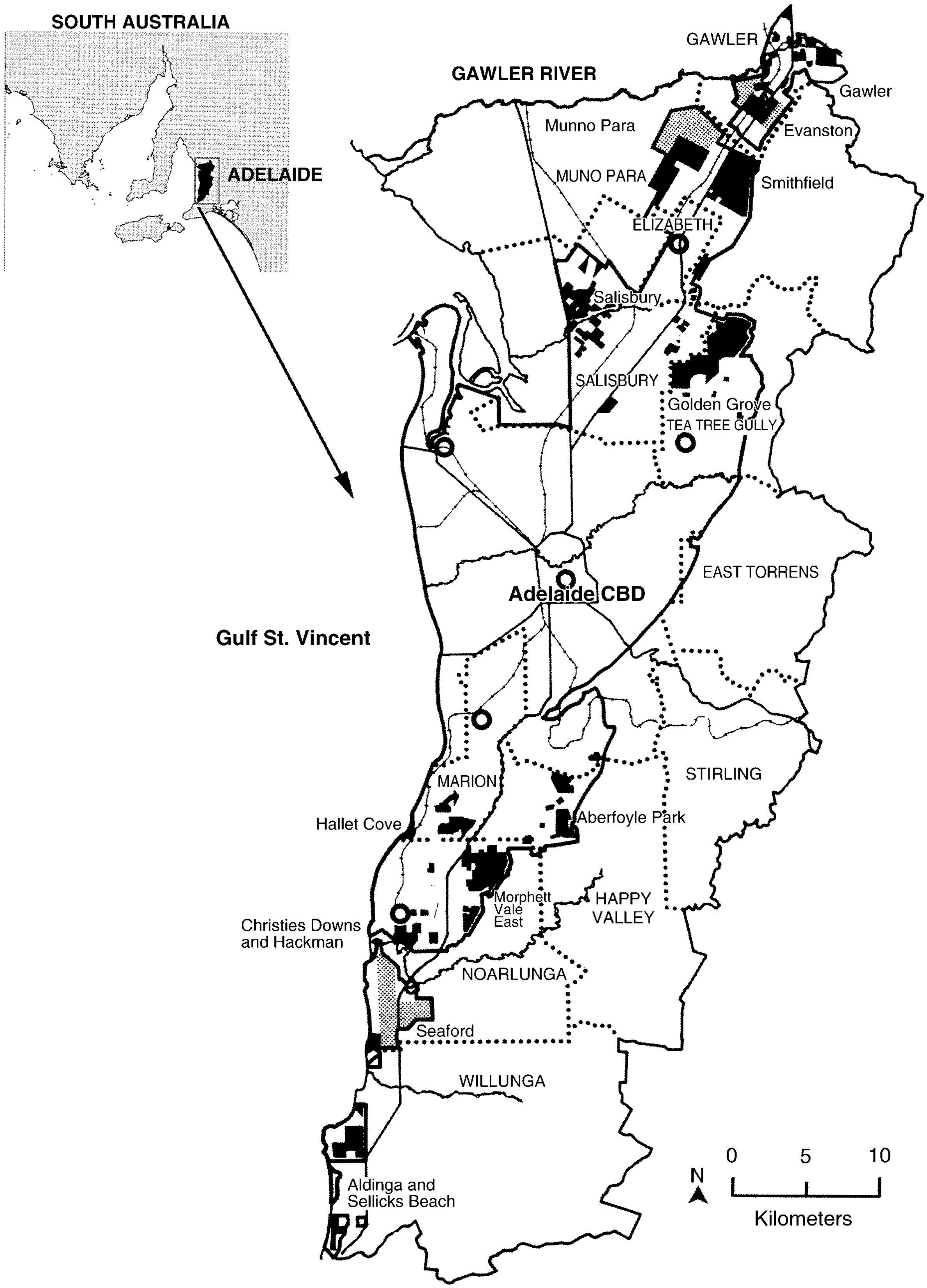

FIG. 1. Map of the Adelaide metropolitan area, Australia (South Australian State Planning Authority 1975).

TABLE 1. Categorization of functional groups separately analyzed.

Initial categories	Subsequent divisions
Plants	native or introduced plant community plant structure geographical origin of introduced species
Birds	native or introduced nomadic or migratory common habitat size (length from tip of bill to end of tail) dominant feeding ecology
Mammals	native or introduced arboreal
Reptiles	native or introduced
Amphibians	native or introduced

were identified from recent checklists, such as those of Paton et al. (1994) and Turner (2001) (see Appendix A for scientific names and authorities of species mentioned within the text). A search of past literature on Adelaide's biota was then conducted. The data were evaluated for reliability by determining whether the author was well known, or highly experienced, in the relevant field. The location of the data and the year in which it was collected were both recorded. More than 180 references were used to create this database (see Appendix B). Of these references, >60 were used for plant information, close to 100 were used for bird information (many were specific studies of only one bird), ~30 were used for mammals, and slightly <20 were used for the reptiles and amphibians (a number of references contained information on more than one of the categories, for example, Turner [2001] had information on all five of the categories). Although <40 of these references were created before 1950, many contained high-quality historical information.

The information was divided into five categories: vascular plants, birds, mammals, reptiles, and amphibians. The native and introduced species were identified (Appendix C), and then each category was divided into functional groups (Table 1), which were separately analyzed. The functional groups chosen were those most likely to be affected by urbanization and its associated impacts. A description of these groups and individual definitions can be found in Appendices D–F. A species was considered absent if a major scientific work considered it as absent (i.e., one written by an expert in their field). Generally, for years after 1950, the data was highly reliable, and more than one data set agreed on the date of loss. Before that time, it was only possible to rely on such experts that undertook surveys in their particular field of expertise (e.g., John Barton Cleland and John McConnel Black for the plants).

As a result of the extended period of time through which data were collected, some problems were encountered concerning species nomenclature. To overcome the obstacle of assigning presence or absence information to species with multiple common names, several sources of information were utilized to identify synonymy. These were Condon (1969), Watts (1990), Cogger and Zweifel (1998), and the Australian Plant Name Index (Centre for Plant Biodiversity Research and Australian National Botanical Gardens, *available online*).[2] Due to the nature of combining data from a large number of sources over a long period of time, some limitations were placed on the nature of data accepted. The information included in the database must have made specific reference to the defined Adelaide area. Some additional definitions were utilized: (1) Native species were defined as those present in the Adelaide area prior to 1836. Natives occur naturally within Adelaide and arrived spontaneously by natural processes before 1836. This definition includes native reintroductions (those native species present in Adelaide in the early years, which then became locally extinct and have since been reintroduced, such as *Dromaius novaehollandiae* [Emu]; Parker et al. 1979). (2) Introduced species were defined as anything not present in the Adelaide area in 1836, including species native to other areas of Australia (or even South Australia), but formerly foreign to the defined Adelaide region.

In some years, only one author had collected data for a particular group. This happened more frequently for the data collected before the mid-1900s. The information was included in the database only if absolutely no other reliable sources could be found for that year, and if the author was a well-known expert in their particular field.

Whilst gardens are an important component of the urban plant community, only garden escapes (plants growing outside the boundaries of artificially maintained gardens) were included in the database (Kent et al. 1999). Including garden plants would have biased the data analysis towards introduced species, especially for data collected in the early years of settlement. As most garden plants do not establish independently growing populations, their inclusion would have obfuscated the important patterns. Hence, only those

[2] ⟨http://www.anbg.gov.au/cpbr/databases/apni.html⟩

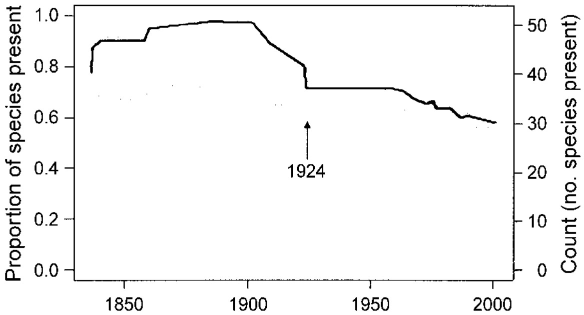

FIG. 2. Calculation of curves on the ''total mammal species'' graph, years 1850–2000. In the year 1924, of a total of 52 species, 32 species were recorded as present, 13 as absent, and 7 as unknown status. The upper line (gray) was calculated to be 39 species (32 + 7), shown on the Count axis, and a proportion of 39/52, or 0.75. The middle line (black) gave a proportion of 0.71, from 32/(32 + 13), thus calculated to be just less than 37 species (0.71 of 52). The lower line (gray) was calculated as 32 species, and had a proportion of 32/52, or 0.62.

The Proportion axis shows the proportion of species present. For the upper and lower curves (gray), this is the proportion of species present compared to the total number of species (present, absent, and not available [NA]). For the central curve (black), this is the proportion of species present compared to the total number of species with known status (present and absent).

The Count axis shows the total number of species present. The upper curve (gray) is the maximum number of species present. The lower curve (gray) is the minimum number of species present. The central curve (black) is the number of species most likely to be present at any given time. The central curve is determined by multiplying the proportion value of this curve at each time point by the maximum number on the Count axis. Hence, the central curve is a measure of the influence of NA values. The closer the central curve is to the upper curve, the more likely that the species classed as NA are actually present. If the central curve is in close proximity to the lower curve, then the species classed as NA are more likely to be absent.

plants found growing in ''natural'' habitats, such as vacant housing blocks, conservation parks, roadsides, and as riparian vegetation were included. Nonvascular plants and invertebrates were excluded from the database, as were data from the soil seed bank, due to a lack of historical species richness data.

Data analysis

To identify the patterns of change, the data were visualized using a system for statistical computation and graphics called R, version 1.6.2 (Ihaka and Gentleman 1996). R is an interpreted computer language that was designed to provide an extensive diversity of statistical linear and nonlinear modeling, classical statistical tests, time-series analysis, clustering, and graphical techniques. The visualization process involved graphing the proportion of non-extinct species against time. Three curves were produced for each graph (see Fig. 2 for an example of calculating each curve). The upper curve, which indicates the maximum possible number of species present in that year, was calculated by adding the total number of species present to the total number of species whose status was not known (i.e., the total number of values for data not available [NA] for that year). ''Data not available'' means no record of the species was found for that year, and in years prior to and after the year in question, the status of the species differs. For example, before the year classed as NA, the species may have been present, whereas after the year classed as NA, the species may have been deemed absent from the area. This also applies to introduced species (classed as absent in 1836) that were not officially recorded in the area until a date later than the year in question. The central line was calculated as a proportion of the number of species recorded as present, in relation to the number of species whose status was known: in other words, the total species present divided by the total number of species recorded as present and absent. This central line highlights the effect that NA values have on the basic pattern. For example, when the central line is closer to the upper curve, it is likely that most of the species with NA values are actually present. The lower line, which indicates the minimum possible number of species present, was calculated by assuming that all species with NA values were absent. The central line is therefore the ''best estimate,'' or the most probable pattern of species richness change over time.

The general pattern in the graphs is that the lower line showed a greater deviation from the central line early in the history of Adelaide, but converged with the central and upper lines in the most recent past. In the 1800s, there was a higher number of species with unknown status due to the smaller number of surveys taken of the biota; thus, less certainty in the data. It was more than likely that the native species were still present in earlier years, but had to be recorded as of unknown status because the records were not taken or kept. In addition, many introduced species were probably established before they were recorded (especially for the plants). Thus, up to around the 1920s, the upper and central lines on the graphs were more likely to be correct than the lower error line (particularly for the mammal, reptile, and amphibian groups).

An illustration of the different manner in which these lines change in response to an extinction event is as follows. Usually a species was more than likely to be extinct before their extinction was actually recorded. Hence, a species tended to be listed as of unknown status (NA) before it was recorded as absent. The initial decrease from present to unknown status of species undergoing extinction produced a decline in the lower line and a smaller decline in the central line. When the species was eventually recorded as absent, the lower line showed no further decrease, while the central line again experienced a slight decline. Thus, the central line in this case was the more appropriate description of the change in species richness because there were probably a few individuals remaining initially, just too

TABLE 2. Total plant, mammal, bird, reptile, and amphibian species numbers in the Adelaide, Australia, metropolitan area during 1836, 1900, 1950, and 2002.

Date	Native			Introduced		
	Present	Absent	Not known	Present	Absent	Not known
Plants						
1836	1136	0	0	4	643	0
1900	1108	5	23	320	153	174
1950	1087	3	46	572	28	47
2002	1047	85	4	617	8	22
Mammals						
1836	40	0	0	0	12	0
1900	30	0	10	6	1	5
1950	22	13	5	10	0	2
2002	20	20	0	9	1	2
Birds						
1836	292	0	0	0	22	0
1900	268	3	21	9	5	8
1950	271	3	18	10	4	8
2002	271	21	0	20	2	0
Reptiles						
1836	56	0	0	0	2	0
1900	56	0	0	1	1	0
1950	56	0	0	1	0	1
2002	54	2	0	2	0	0
Amphibians						
1836	7	0	0	0	0	0
1900	7	0	0	0	0	0
1950	7	0	0	0	0	0
2002	7	0	0	0	0	0

few to be seen and recorded, hence extinction occurred some time in that period.

The lower error line and the central line tended to meet in more recent years because more (and more complete) records were kept, thus, a better knowledge of the present and absent biota was possible. The number of species recorded as unknown status was lower in recent years, hence the upper curve (total species present plus the number of species with unknown status) fell, while the lower error line rose to join the central line. There is less error in the data today than at either settlement or the turn of the 20th century.

Data was extrapolated between data points to provide the continuous graphical representation. For example, if in 1890 a species was recorded as present and the same species was recorded as present in 1910 (and there were no data sets for the intervening years), then it was presumed that the species was present in all years between these two time points. If a species was recorded as present in 1890, but recorded as absent in 1910 (and again there were no data sets for the intervening years), then the species was given the data label NA for the intervening years.

RESULTS

Overall biodiversity

Table 2 is a summary of species richness at four time points. The particular years were chosen to represent four fairly evenly spaced time intervals when there was a great deal of change occurring (at settlement, at the turn of the century when many mammal populations appear to have dramatically declined, in the housing and industrial boom after the two world wars, and the picture today). The data for 1836 is from very recent, very complete checklists (1990–2002) stating which species are native and which are introduced. The data for 1900 is extrapolated from years prior to and after this date. The data for 1950 is extrapolated for the birds, mammals, reptiles, and amphibians, while many of the plant species are recorded from seven surveys undertaken in that year. The data for 2002 are direct records from surveys in 2001 and 2002.

The native species have decreased in all groups except the amphibians. Native plant species numbers have decreased by 7.5%, mammals by 50%, birds by 7.0%, and reptiles by 3.5%. The number of exotic species introduced, as a percentage of the number of native species, is 54% in plant species, 23% in mammals, 7.0% in birds, and 3.5% in reptile species. This indicates that there is an overall increase in plant species richness (46%), an overall decrease in mammal richness (27%), and no change in the total bird and reptile species richness.

Plants.—Overall, there was an increase in species numbers (Table 2). There were two periods of rapid species increase, 1836–1838 and 1856–1858 (Fig. 3A). In the two years between 1836 and 1838, there were 13 definite introductions and 154 possible introductions

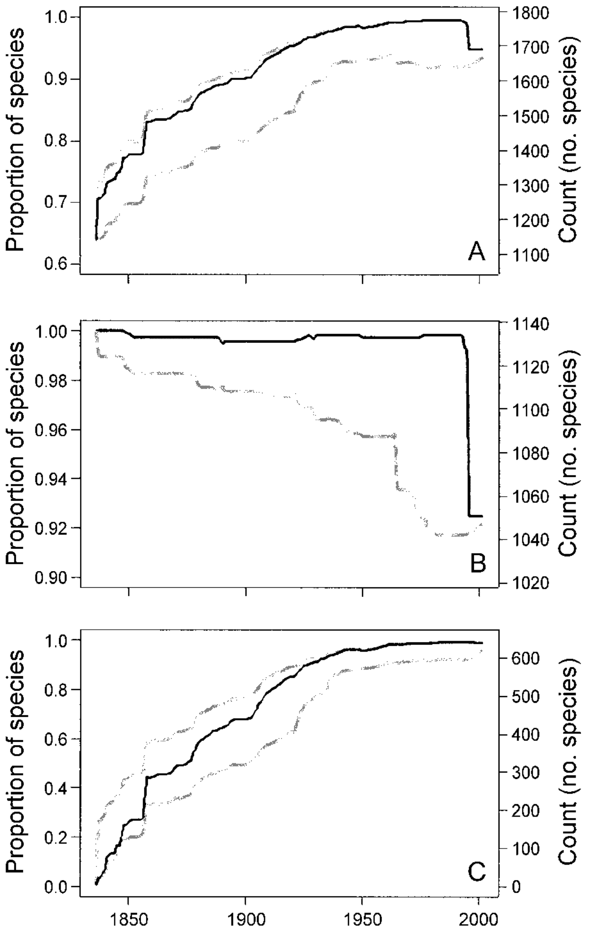

FIG. 3. Changes in plant species richness observed in the Adelaide area from 1836 to 2002: (A) all observed species, (B) native species, and (C) introduced species. The Proportion and Count curves are described in Fig. 2.

(exact date not known). This jump in species richness was not shown on the lower error line (NA = 0) since the 154 species were categorized as data not available, or NA. During 1856 to 1858 there were 84 recorded plant introductions. Species richness was also increasing fairly rapidly between these two periods: from 1143 species in 1838 to 1248 in 1856, a jump of 105 species, or a 9% increase. From 1871 to 1902, an increase of 76 species occurred (with 13 more species whose presence or absence was not known). The rate of increase accelerated slightly between 1902 and 1920 (4.5 species/yr) and then remained fairly constant to 1960 (4.0 species/yr). From 1960 to 1996, species numbers slightly decreased (0.78 species/yr), but with gradually more and more species whose presence or absence was not known. The large decrease recorded in 1996 is the result of an excellent survey that determined the fate of many plant species. In 1996, 85 species were recorded as absent, whereas previously their existence in the Adelaide area had not been known. These plants were probably extinct in the Adelaide area well before 1996. As a result, it is highly likely that the lower error line is the most accurate description of this decrease in species numbers.

The number of native plant species remained relatively constant from 1836 (1136 species) to 1995 (1125 species), a decrease of only 1% (Fig. 3B). The lower error line decreased slowly from 1922 until 1964, when there was a rapid decline in species numbers (Fig. 3B). In 1990, 92 species were not recorded as present or absent. However, in 1996, only eight species could not be categorized in this way (see description of Fig. 3A above).

The initial jump in numbers from 1836 to 1838 seen in Fig. 3A was not replicated in the central line of Fig. 3C. The upper error line, however, increased from four to 171. At this time, there were 154 species whose presence or absence was not established. The actual number of species recorded as present in this period increased from four to 17, causing the lower error limit to be closer to the correct pattern of species richness change. The number of introduced plant species remained fairly constant from ~1970 to the present, with only ~20 further introductions in the entire 32-year period to 2002.

Birds.—Although there were periods of increase and decrease, the total number of bird species present in 1836 (286 species) was similar to that in 2002 (283 species) (Fig. 4A). The dip at 1878 is because 18 species of bird were recorded as absent, with 14 of unknown status (compared to there previously being nine species absent and 24 of unknown status). The major decline in species richness began in 1959. From then to 2002, 15 species were lost. Six species (*Lophoictinia isura* [Square-tailed Kite], *Pavo cristatus* [Indian Peafowl], *Poephila acuticauda* [Long-tailed Finch], *Motacilla cinerea* [Grey Wagtail], *Pycnonotus jocosus* [Red-whiskered Bulbul], and *Pezoporus wallicus* [Ground Parrot]) were lost in the previous 123 years. The lower error line slowly rises to meet the central line because the status of more and more species is known, reducing the error in the data.

Native bird species richness (Fig. 4B) closely follows the line of Fig. 4A. The slight increase in 1912 seen on both graphs was therefore also due to native species. The decrease in species numbers from 1959 to 2002 was almost identical in Fig. 4A and B, apart from the small variation during 1982–1986, and the final slight increase in species numbers in 2001 seen only in Fig. 4A.

The initial increase in introduced species richness occurred in 1868 (Fig. 4C). The upper error line rose initially because 13 species had unknown status. The jump in 1952–1953 was a result of three species being recorded as present (*Ocyphaps lophotes* [Crested Pigeon], *Anas platyrhynchos* [Mallard], and *Acridotheres tristis* [Indian Mynah]). After 1953, there was a general change from unknown status to present, thus reducing the lower limit error (bringing it closer to the actual

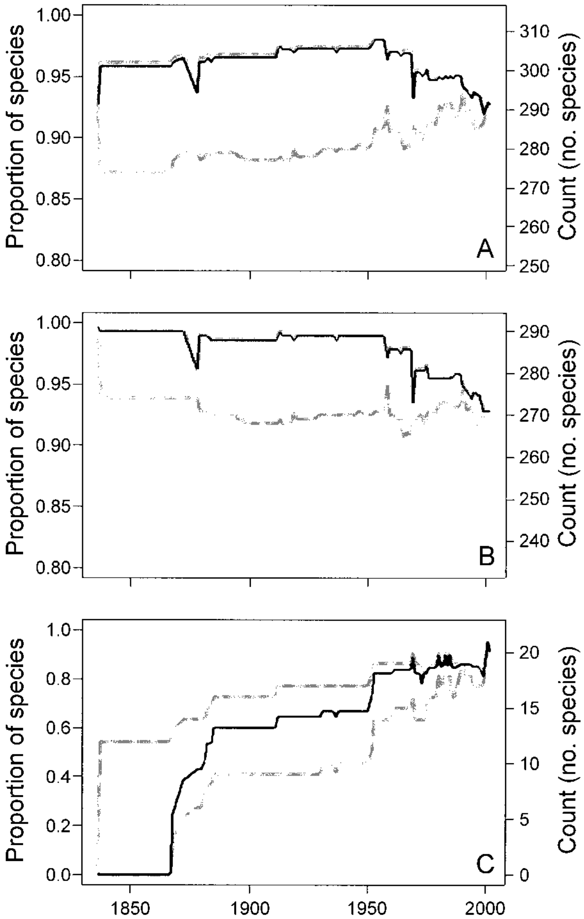

FIG. 4. Changes in bird species richness observed in the Adelaide area from 1836 to 2002: (A) all observed species, (B) native species, and (C) introduced species. The Proportion and Count curves are described in Fig. 2.

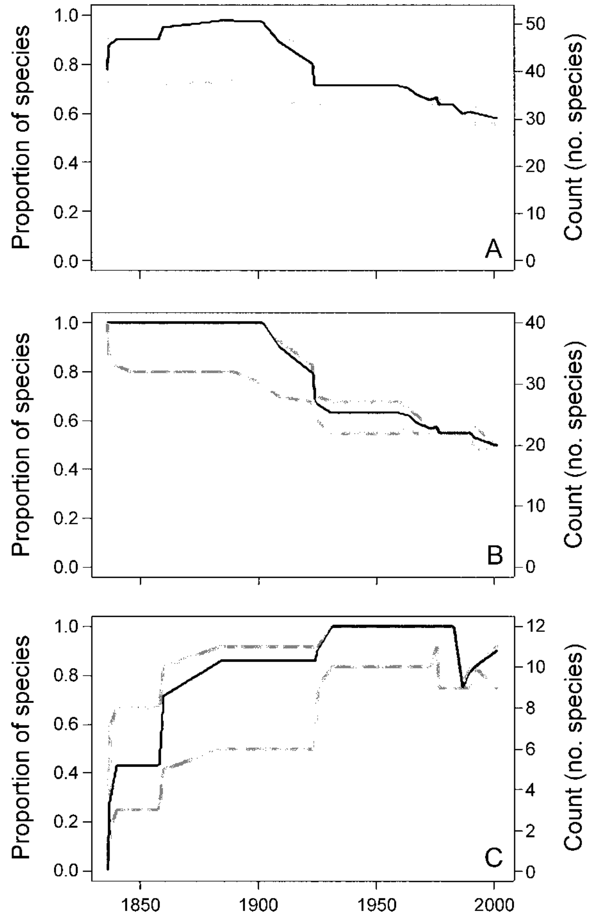

FIG. 5. Changes in mammal species richness observed in the Adelaide area from 1836 to 2002: (A) all observed species, (B) native species, and (C) introduced species. The Proportion and Count curves are described in Fig. 2.

value). The final jump in 2001 was a result of some species being recorded as present when previously absent. There was a greater number of observations for the more recent time periods and thus more chance that certain introduced species (such as the Indian Mynah) would be located if they were present.

Mammals.—A decline from 40 to 29 species present, or a 27.5% decrease, was observed in the mammal group (Fig. 5A). Initially, there was an increase in species numbers between 1836 and 1840 (three species were introduced: *Capra hircus* [feral goat], *Felis catus* [feral cat], and *Sus scrofa* [feral pig]) and 1858–1860 (a further two species were introduced: *Oryctolagus cuniculus* [European rabbit] and *Vulpes vulpes* [European red fox]). From 1902 to 1931, there was a loss of four species from present to absent status, as well as the loss of eight species from unknown status to absent. A period of stasis occurred from 1931 to 1960, when no species were lost or gained. From 1960 to 2002, a slow decrease in species numbers occurred, with the loss of the introduced *Canis lupus familiaris* (wild dog) and feral goat, as well as the native *Sminthopsis crassicaudata* (fat-tailed dunnart), *Vombatus ursinus* (common wombat), *Acrobates pygmaeus* (feathertail glider), *Canis lupus dingo* (dingo), and *Conilurus albipes* (white-footed tree-rat).

The first native mammal species to be listed as absent occurred in 1909 (*Macropus robutus* [euro], *Bettongia penicillata* [brush-tailed bettong], and *Dasyurus maculatus* [spotted-tailed quoll]; Fig. 5B). The drop from 1909 to 1931 follows that of Fig. 5A, with a decline of 0.27 species/yr. A slight decline was observed between the years 1960–1977, when the white-footed tree-rat, dingo, feathertail glider, and common wombat moved from unknown status to absent. Between 1990 and 2002, there was again a loss of species, with *Notomys mitchellii* (Mitchell's hopping mouse), *Cercartetus concinnus* (western pygmy-possum), and the fat-tailed dunnart no longer present.

There were three major periods of introduction for mammals (Fig. 5C): 1836–1840, 1858–1884 (a combination of two increases in species numbers, 1858–

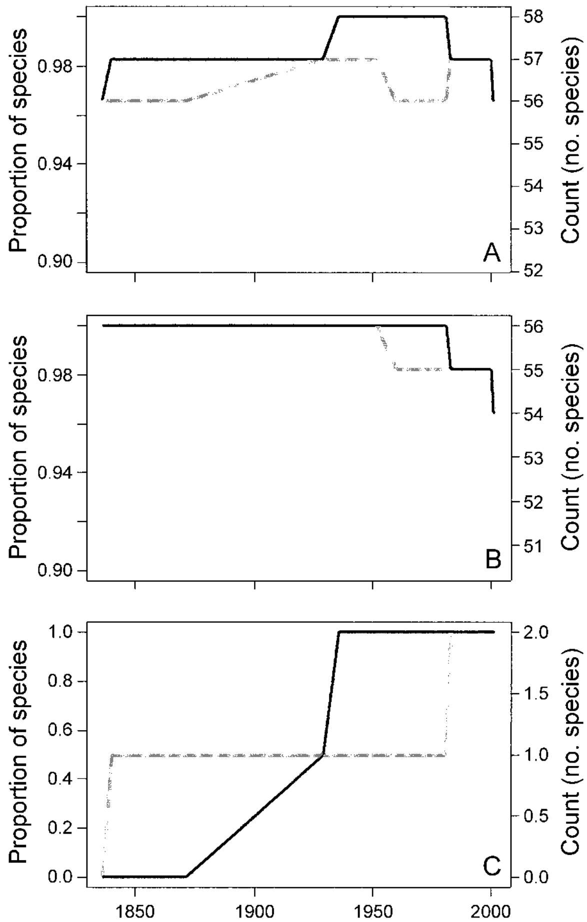

FIG. 6. Changes in reptile species richness observed in the Adelaide area from 1836 to 2002: (A) all observed species, (B) native species, and (C) introduced species. The Proportion and Count curves are described in Fig. 2.

1860 and 1860–1884), and finally 1925–1931. There was no change to species richness between these jumps. A total of 12 mammal species were introduced into the area.

Reptiles.—There was no overall change in reptile species numbers (56 species present in 1836 and in 2002; Fig. 6A). Two introduced species of reptile (*Chelodina longicollis* [common long-necked tortoise] and *Physignathus leseurii* [water dragon]) were first recorded as present in 1929 and 1983, respectively, while two native species were lost by 1983 and 2001 (*Tiliqua adelaidensis* [pygmy bluetongue] and *Acanthopis antarcticus* [common death adder] respectively) (Fig. 6B). Fig. 6A and C indicate that some time in the period between 1836 and 1929 (when initially recorded as present), the common long-necked tortoise arrived. The water dragon arrived some time between 1936 and 1983. Fig. 6B indicates that within the period between 1960 (when first recorded as unknown status) and 1983 (when finally recorded as absent), the pygmy bluetongue went extinct. Therefore, Fig. 6A, between the years 1836–1983, is representative of the introduced species change, and follows the pattern of the native species change from 1983 to 2002.

Amphibians.—There was no change recorded in the total number of amphibian species. No amphibians were introduced from outside the Adelaide area and none of the seven native amphibian species have yet become locally extinct. The number of data sets gathered for this group was lower than for the other classes due to a relatively small number of checklists produced historically and in the recent past (roughly nine over the last 30 years). However, the lack of change in species numbers is unequivocal.

Specific groups

Plants.—The annual and herbaceous perennial groups showed a fairly constant increase in species numbers followed by a recent loss of native species (Appendix C, Fig. C1C). The tree group experienced introductions with no loss of native species (Appendix C, Fig. C1B). By 2002, the number of native species in all three groups was far outnumbered by the number of introduced species (illustrated by Fig. C2A in Appendix C). Around a third of the introductions for both the annual and herbaceous perennial groups occurred within the first 20 years of settlement. The aquatic and glabrous perennial guilds both experienced early introductions, followed by a period of stability, and then recent loss of native species, resulting in an overall increase in species numbers, similar to the annual and herbaceous perennial groups (Appendix C, Fig. C1D). Despite the majority of absent recordings occurring in 1996, most of the extinctions for these groups probably occurred before 1973.

The climber and tall shrub groups experienced introductions with no loss of native species (Appendix C, Fig. C1B), so that by 2002 there were still more natives than introduced species (illustrated by Fig. C2C in Appendix C). Conversely, there were only native species in both the erect perennial and orchid guilds, and these declined recently in species numbers.

The grass and sedge layer, low shrub layer and perennial guilds all had a small number of early introductions, followed by a period of stability, and then recent loss of native species (Appendix C, Fig. C1E). The shrub group showed a fairly constant increase in species numbers followed by recent loss of native species (Appendix C, Fig. C1C). Despite the loss of native species and arrival of exotic species, all four guilds showed a larger proportion of native species remaining by 2002 (illustrated by Fig. C2B in Appendix C). The shrub species showed the fastest introduction rate of any group.

Birds.—The carnivorous, piscivorous (Appendix C, Fig. C4H), and aquatic organism-feeding bird species have experienced minimal change in species richness. The number of granivorous bird species in the Adelaide area doubled. The herbivorous and omnivorous bird species have declined in numbers after an initial increase. The insectivorous birds and those that feed on both insects and nectar (Appendix C, Fig. C4E, F) showed similar patterns, with little change in species richness until the mid-1900s, when a decrease was observed.

The coastal (Appendix C, Fig. C5A), open woodland, and marine (Appendix C, Fig. C5C) bird species showed very little overall change in species richness. Birds commonly found in dense scrub, freshwater (Appendix C, Fig. C5B), and open plains habitats (Appendix C, Fig. C5D) increased in species numbers overall, with an initial increase (the arrival of exotic species) followed by a period of relatively little change, and then a decrease in numbers after 1960 (for freshwater and open plains birds). The number of bird species regularly found in suburban areas (Appendix C, Fig. C5G) experienced a sharp increase (with the arrival of six exotic species) without the loss of any of the three native species (*Gymnorhina tibicen* [Australian Magpie], *Hirundo neoxena* [Welcome Swallow], and *Phylidonyris novaehollandiae* [New Holland Honeyeater]). The woodland birds encountered the greatest species decline of any of the groups, with a loss of 15% of the original species total.

Mammals.—Five of the 18 native species found within the arboreal group were extinct by 2002, a 28% decline (*Phascogale tapoatafa* [brush-tailed phascogale], western pygmy-possum, feathertail glider, *Miniopterus schribersii* [common bent-winged bat], and white-footed tree-rat; Appendix C, Fig. C7A). There were only three species in the partly arboreal mammal group (Appendix C, Fig. C7B), and all of these were native (spotted-tailed quoll, *Dasyurus viverrinus* [eastern quoll], and *Antechinus flavipes* [yellow-footed antechinus]). For a period of 13 years (between 1977 and 1990) all three species were locally extinct in the area, a loss of 100%.

In 2002, the ground-dwelling mammal group had 14 species present, 14 absent, and 2 of unknown status (feral goat and *Cervus dama* [fallow deer]; Appendix C, Fig. C7C). There were originally 19 native and 11 exotic species. A total of 13 native terrestrial mammal species were extinct by 2002 (e.g., *Ornithorhynchus anatinus* [platypus], *Myrmecobinus fasciatus* [numbat], fat-tailed dunnart, *Macrotis lagotis* [greater bilby], *Perameles bougainville* [western barred bandicoot], *Lasiorhinus latifrons* [southern hairy-nosed wombat], common wombat, and the dingo), a 74% reduction in the number of native terrestrial species.

Discussion

Historical and current species richness information was used to create a temporal ecological study relevant to current management practices. By demonstrating change over time, an understanding of the dynamics involved in ecological succession is gained, especially in disturbed environments such as urban areas.

There was nearly a 30% increase in the number of animal and particularly plant species present. However, there has been significant loss of native species within all but one of the groups, at the same time as the introduction of exotic species. These changes are discussed with reference to individual groups of plants and animals.

Specific groups

Plants.—No one particular plant family experienced particularly high declines in species numbers. The introduced species were also relatively evenly dispersed among the families. Thirty-eight of the 146 families (<30%) in the Adelaide area contained only introduced species. Families that experienced a decline in the proportion of species recorded as present from 1836 to 2002 were the Ranunculaceae, Orchidaceae, Marsileaceae, Haloragaceae, Goodeniaceae, Campanulaceae, and Menyanthaceae. The large numbers of introduced plants could also be a result of the high levels of many soil nutrients, such as phosphorus, in the urban area. These concentrated nutrient supplies can promote the invasion of exotic plants and enhance changes in the composition of urban native plant communities (King and Buckney 2002).

Agriculture and grazing were especially important mechanisms of native vegetation removal from the early years of settlement. A grazed area is characterized by changes to the composition and structure of the ground flora and often by a decline in, or removal of, native shrub species, herbaceous perennial species, and grass tussocks (Ford et al. 2001). Changes to the chemical and physical properties of the soil, particularly when there is a relatively high clay content (as in certain areas of the Adelaide region), are also a side effect of grazing (Hobbs 2001). When the soil is trampled, it reduces the regeneration ability of tree species, particularly from woodland systems. The plant community most destroyed by agricultural and grazing practice was the box grassy woodlands that used to dominate the Adelaide plains (Davies 2000). Due to their location in areas of reliable rainfall, these woodlands were targeted for agricultural development, and as open systems they were preferred grazing areas. Selective grazing of the more palatable plant species by stock was shown to be responsible for reducing the native species richness and changing community composition. For example, differences in location of both *Eryngium rostratum* (native celery) and *Microseris lanceolata* (yam daisy) were related to grazing intensity (McIntyre 1995).

Fragmentation of an area increases edge habitat and leads to entry points for aggressive exotic species that can not only displace native species (Hobbs 2001), but also alter soil characteristics (particularly legumes that fix nitrogen in the soil). The invasion of these weedy exotics also inhibits the ability of many specialized native species to reinvade after disturbances such as fire (Australian SoE Committee 2003). In addition, opening up a habitat by increasing the number of access roads will change the microhabitat climatic features, resulting in greater air movement, lower humidity, soil erosion, and soil drying (Drayton and Primack 1996). There has, however, been no further remnant vegetation clearance in the Adelaide region since the mid-1980s (Paton et al. 1994). The initial vegetation removal may have decreased the viable populations of species, which then were further affected by the decreases in propagule dispersal. This may have been followed by increased competition with introduced species for limited resources, eventually leading to the extinction of particular species.

It is conceivable that, after the vegetation clearance and habitat fragmentation in Adelaide, the survival of some species is now dependent on habitat islands within the metropolitan area, which are isolated from other similar biological communities (Drayton and Primack 1996). If a plant species went locally extinct (due to fluctuations in the natural demography, successional changes, or human activity) in one area of Adelaide, natural recolonization may in fact be impossible if there were isolated habitat islands. This is especially important for short-distance disperser plant species (e.g., dispersal of reproductive material by ants).

Invasive plant species (those that negatively impact on resident species) have the potential to significantly change the function and composition of an ecosystem (Hobbs 2001). Invasive species have had profound economic and cultural consequences worldwide (Vermeij 1996). The invasion of weeds could cause problems for native vegetation, especially in relation to the regeneration of dominant woody types. The establishment of native seedlings is significantly reduced in the presence of annual weedy species (Hobbs 2001). Declines in native species richness once the non-native species cover has exceeded 40% were evident in urban remnant grasslands from southeastern Australia (Morgan 1998). The native species directly or indirectly affected by the presence and spread of exotic species must cope with and respond to the changing ecological processes that occur with the development of novel communities and community structures, or suffer the consequences of restriction and even extinction (Vermeij 1996). The greatest proportional loss of native species (14%) occurred within the herbaceous perennial and glabrous perennial groups, closely followed by the annual and aquatic groups (13%). The highest levels of introductions occurred within the annual, herbaceous perennial, and tree groups, with a 230% increase on the original total for the annuals, and 160% increase for both the herbaceous perennial and tree groups.

The annual and herbaceous perennial groups have been the most dynamic, experiencing the highest levels of extinctions and introductions. The annuals have a shorter growing and flowering season, thus can spread more quickly, reducing the possibility of quick and efficient eradication. Competition for resources (both biotic and abiotic), accompanied by changes in pollinator-use could then have contributed to the high number of recorded extinctions for both the annual and herbaceous perennial groups.

It is possible that the longevity of tree species, in comparison to annual and herbaceous perennial species, has created high rates of introductions with no loss of native species. However, this may be a consequence of a long time lag between introduction and extinction, so that it will be important to monitor tree populations as well as their species richness.

Birds.—The recent decline in native bird species almost equaled the increase in species numbers via introductions (21 native species went extinct and 20 introduced species arrived). This was in contrast to the warnings of Recher and Lim (1990), who predicted the decline and extinction of Australian birds to parallel that shown by mammals over the last 100 years.

The greatest rates of bird extinction have been occurring over the past 30 years. Some possible reasons for this recent decline include the loss of relatively unfragmented habitat outside the metropolitan area, changes in urban predators, and changes in the nature of the habitat within the metropolitan area, but outside the bushland reserves. Changes in the composition of bird species have also occurred as a consequence of the loss of understorey plant species (which many small woodland birds utilize as habitat and as the preferential feeding location; Paton et al. 2000).

Australian birds are thought to be relatively long lived, implying that small but nonviable populations of species may have persisted in urban vegetation remnants for long periods before they disappeared (Ford et al. 2001). This could explain the extended time without species loss, followed by the recent rapid decline in species richness (Fig. 4A).

The native insectivorous passerines dependent on native vegetation have undergone particularly high declines in species numbers, as shown by Ford et al. (2001). It can be assumed that plant species declined in the abundance before their extinctions were recorded, possibly inhibiting the foraging ability of the small birds that use them. Hence, plant declines probably lead to population declines and subsequent extinction of birds. Many birds are associated with one or only a few habitats, and management problems occur when these particularly important habitats are preferentially removed (as has occurred in the Mount Lofty Ranges). The loss of the best quality sites can lead to a disproportionate loss of both individuals and species (Ford et al. 2001).

The higher proportion of edge to center habitat in fragmented, remnant vegetation has influenced which bird species would survive (Ford et al. 2001). Thus, in the fragmented habitat of Adelaide, the birds that thrive in edge-type environments, especially aggressive birds (e.g., *Manorina melanocephala* [Noisy Miner]) will be less likely to go extinct. The species observed to be edge-avoiders by Ford et al. (2001), were mostly the small insectivores, providing a possible explanation for their observed decline (Appendix C, Figs. C4E and C6A).

Mammals.—Australia has the worst record for mammal conservation of any country or continent in the world, claiming half of all the mammal extinctions worldwide over the past 200 years (Short and Smith 1994). Adelaide's native mammal species experienced a loss of 50% by 2002, with extinctions of 20 of the 40 native species. This extraordinarily large decline in species numbers was probably the result of a combination of factors, such as the introduction of hunting by Europeans, clearing and fragmentation of native vegetation, grazing by rabbits, and stock (both feral and domestic), altered fire regimes, and increased predation from introduced species such as foxes and cats (Short and Smith 1994). The impact of hunting was probably not as important to the observed species decline in Adelaide as was the invasion of introduced rabbits and foxes, and changes in the land use and land management practices within Adelaide (Short and Smith 1994). Currently, no mammal species in Adelaide are believed to be threatened by trade or hunting since the enactment of state legislation early last century.

Most of the recorded extinctions in the Adelaide metropolitan area were from two taxonomic groups: marsupials and rodents. However, the local extinction of the platypus was a loss of half of the native monotreme species (*Tachyglossus aculeatus* [short-beaked echidna] is still present). No mammal habitats in Adelaide have been completely cleared, so none of the extinctions can be attributed entirely to the clearing of native vegetation. The fragmentation of populations into smaller groups (through the clearing and dissection of habitat) might have heightened the possibility of extinction, which was then caused by other disturbances (Short and Smith 1994).

A time lag of ~30 years was observed between the arrival of most of the introduced mammals into Adelaide and the beginning of the decline in the native mammals. This suggests that there is a period of ~30 years after the arrival of introduced species in which to save native mammals from extinction, providing appropriate management policies are implemented.

Almost all the medium-sized, ground-dwelling marsupials (e.g., bettongs and quolls in the weight range 35.0 g to 5.5 kg) became extinct in the Adelaide region (Short and Smith 1994). These species are known as the critical weight range species (CWR; Turner 2001). The terrestrial species (Appendix C, Fig. C7C) were more susceptible to predation, particularly from the introduced fox and cat, than were the flying species (bats) and arboreal species (possums and gliders) (Short and Smith 1994). Species richness of native herbivores may have decreased as a result of the introduction of foxes and cats, or due to their replacement by introduced herbivores (rabbits), as in the case of southwestern Australia (Hobbs 2001).

The decline of Adelaide's CWR species has been attributed in part to the effects of grazing reducing the availability of food resources and shelter from predation (by removing the understorey layer; Short and Smith 1994). The local extinctions of many mammals were also attributed to foxes, feral cats, and rabbits, which effectively alter physical and ecological characteristics of the habitat (Dickman 1996). Rabbits enhance the negative impacts of introduced predators by supporting large predator populations (Dickman 1996). During the period of rabbit (and fox) introduction and spread, there was also large-scale clearing of native vegetation in Adelaide for agricultural and grazing purposes. The definitive impact of these introduced mammals on native fauna species richness was thus compounded by the reduction and fragmentation of local habitat occurring simultaneously (Hobbs 2001).

Reptiles.—The total reptile species richness did not change from 1836 to 2002. Two species were introduced (the common long-necked tortoise, an amphibious, nocturnal species; and the water dragon, an arboreal, diurnal species), and two native terrestrial species from a total of 56 became extinct (the nocturnal common death adder, and the diurnal pygmy bluetongue). The common death adder was only lost recently (2001), while the pygmy bluetongue has not been recorded in the Adelaide area since 1952.

Studies of reptile habitat preference highlight the importance of substrate type and the physical structure of the environment rather than the specific vegetation type (Robinson 1986). Thus, changing the vegetation type of the Adelaide area through the extinctions and introductions of plant species may not have had as significant an impact on the reptile fauna as on the birds and mammals, resulting in the minimal change to reptile species numbers.

Amphibians.—None of the seven native amphibian species became extinct after 166 years of significant habitat alteration and pollution to the waterways throughout the entire Adelaide area (Warburton 1977). It would be impossible to find a creek in pristine condition because of the influence of both direct and indirect pollution. One native species of amphibian (*Litoria raniformis* [southern bell frog]) has re-established a breeding population in Salisbury, located on the northern Adelaide plains, after being absent from that area for many years (Robinson 1986). This highlights the potential for successful reintroduction of mammal, bird, and reptile species into the Adelaide area.

Conclusion

This database is robust and complete enough to generate testable hypotheses and plausible explanations for the establishment of patterns in urban ecology. In this study, the patterns of change in species richness have been observed and described. Adelaide has lost many of its native species over the last 166 years, but has also gained at least 617 new species of plant (mostly annual, herbaceous perennial, shrub, and tree species), 12 mammal, 20 bird, and 2 reptile species. Total species richness has greatly increased, but this increase has slowed. Plants, reptiles, amphibians, and birds have fared better than mammals. Amphibians seem to have done the best, without any recorded extinctions, despite severe alterations to habitats. Declines in native species richness have been attributed predominantly to the disproportional clearance of prime habitat regions through the development of urban, agricultural, and grazing practices. In the past, Adelaide was not managed to protect biological diversity, but rather for economic development. However, the sustainability of the Adelaide region is now a priority for land managers. A long-term management goal is the reintroduction of locally extinct native species, if enough suitable habitats remain (or can be created) free from predators and other harmful impacts. Otherwise, management of the remaining species and communities need to be the main priorities. This study has shown the importance of examining both the introduced and native species found in urban areas, and their interactions. Approaching urban ecological studies in this way will enable us to gain a better understanding of the behavior of exotic species in cities, which is of crucial importance since cities serve as primary immigration sources from which introduced species can spread further into the landscape (Pysek 1998).

Studies of urban environments using historical analyses have been relatively neglected, especially within Australia, where urban areas hold ~85% of the population. Cities should be considered as a new environment with species compositions and habitats highly distinct from rural or natural areas. As the world's population increasingly includes people with an urban lifestyle, it is predominantly in this urban environment that they will gain their views on nature. If all the flora and fauna are portrayed in a negative light because of a lack of scientific knowledge, the average city dweller will not appreciate the richness and diversity of life around them.

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APPENDIX A

A table listing the authorities and scientific names of species mentioned within the text is available in ESA's Electronic Data Archive: *Ecological Archives* A015-010-A1.

APPENDIX B

A list of references used in the creation of the database is available in ESA's Electronic Data Archive: *Ecological Archives* A015-010-A2.

APPENDIX C

A list of figures describing changes to the species richness of particular species guilds is available in ESA's Electronic Data Archive: *Ecological Archives* A015-010-A3.

APPENDIX D

A table giving a description of the plant structural classes is available in ESA's Electronic Data Archive: *Ecological Archives* A015-010-A4.

APPENDIX E

A table giving a description of the bird feeding groups is available in ESA's Electronic Data Archive: *Ecological Archives* A015-010-A5.

APPENDIX F

A table giving a description of habitat areas in which birds sightings were commonly recorded is available in ESA's Electronic Data Archive: *Ecological Archives* A015-010-A6.