ORIGINAL ARTICLE

Land-use changes and monk parakeet expansion in the Pampas grasslands of Argentina

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ABSTRACT

Aim The monk parakeet, *Myiopsitta monachus* (Boddaert, 1783), is a successful invasive species that has established viable populations on four continents, including North America and Europe. Of particular interest is the little known, large-scale expansion of monk parakeet within its native range on the Pampas grasslands of Argentina during the 20th century. To understand the key factors involved in this large-scale expansion and their implications in terms of current hypotheses on bird introductions, we investigated in detail the expansion process and related changes in land use during the period 1860–2010.

Location The Pampas grassland ecoregion of Argentina.

Methods Range expansion was assessed using the following information sources: museum specimens, published scientific literature, reports from government agencies, postal questionnaires, internet public media, and data obtained during extensive travelling by the authors.

Results The range of the monk parakeet has expanded by about 327,958 km^2 in 150 years. The linear range expansion rate was between 2.1 and 7.6 km year^{-1}. Range expansion followed a neighbourhood diffusion pattern. Key land-use changes included expansion of eucalyptus trees (the preferred nesting tree), introduction of European cattle, weed (thistle) invasion, conversion of grassland to cropland, and urban development.

Main conclusions Eucalyptus was a key factor favouring parakeet range expansion. Food availability increased as a result of changes in grassland structure, weed invasion and cropland expansion. Urban environments operated as expansion stepping stones along the routes of railways. The invasive potential of monk parakeet and other parrots appears to be related to behavioural flexibility and dietary opportunism favoured by high intelligence and morphological adaptations (beak and foot structure).

Keywords
Agriculture, Argentina, biogeography, biological invasions, eucalyptus, *Myiopsitta monachus*, Psittacidae, railways, range expansion, thistles.

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INTRODUCTION

The reasons why some birds succeed and others fail to expand into new areas outside their original distribution have still not been entirely elucidated (Blackburn & Duncan, 2001). Although the number of exotic species continues to grow worldwide, even widely accepted predictive patterns are still under scrutiny. For example, Blackburn & Duncan (2001) have shown that for birds the outcome of introduc-

tions is not predicted by general features of locations related to biotic resistance (such as latitude), and that the success of a species cannot be predicted from that of its relatives. Contrarily, it has been concluded that, in addition to environmental suitability, species-level traits associated with introduction success must be phylogenetically labile, varying even among closely related species, instead of being a general aptitude among members of the same family (Blackburn & Duncan, 2001; Duncan *et al.*, 2003; Sol *et al.*, 2012).

Accordingly, further advances in the understanding of biological invasions need to be focused on an in-depth analysis of species-specific situations, in which general concepts and models can be tested and improved (Sax *et al.*, 2007). Moreover, modelling the ecological niche and potential dispersal of invasive species requires reliable data on the ecological characteristics of the species and on their distribution in their native area (often unknown or only poorly known), as well as a good understanding of the key characteristics that determine the degree of habitat suitability provided by that area. Clearly, a lack of validation in the field limits further advances in research on modelling the predictive distribution of invasive species (Baguette & Dyck, 2007; Sax *et al.*, 2007).

Seen from that perspective, an interesting case for analysis is the South American monk parakeet, *Myiopsitta monachus* (Boddaert, 1783), a very successful invasive species that has already expanded to several countries in South, Central and North America, as well as to Europe, the Caribbean and Japan, mostly because of the pet trade (Carrete & Tella, 2008). In addition, in both native and invasive sites the monk parakeet is considered to be a problem for agriculture as well as for electricity transmission lines (Bucher, 1992; Pruett-Jones & Tarvin, 1998).

The monk parakeet is unique among parrots because of its ability to build bulky communal nests for roosting and nesting, therefore being independent of tree or cliff cavities, the nesting habitat required by most parrots. Research from the native population in Argentina indicates that monk parakeets are year-round residents, showing marked philopatry and limited natal dispersal (Martin & Bucher, 1993).

The monk parakeet underwent a very significant range expansion in its native area during the 20th century, particularly in the Pampas grasslands of Argentina (Forshaw & Cooper, 1989). This expansion was coincident with major environmental changes introduced by the European settlement of the area, particularly conversion of the original grasslands into croplands, which had significant effects on the original biodiversity. Information on the monk parakeet expansion is limited to brief comments in the scientific literature (Forshaw & Cooper, 1989). Fortunately, historical records allow a fairly accurate reconstruction of the expansion process and the associated land-use changes.

A comprehensive analysis of this large-scale range expansion event may contribute to filling an information gap, with wide implications. According to Strubbe & Matthysen (2009), lack of information of the native range prevents valuable insights into the key habitat requirements of a species (Sax *et al.*, 2007). The analysis of the invasive process of the monk parakeet in its native range may also provide useful information and insight regarding more general questions, such as identifying adaptive characteristics of successful invasive species. This matter is particularly interesting in parrots, one of the most highly threatened families in the world, which at the same time has more invasive species than would be expected by chance (Lockwood *et al.*, 2000). An impor-tant open question is whether or not long-distance dispersal occurs in the monk parakeet native area, given that Gonçalves da Silva *et al.* (2010) found genetic evidence for significant long-distance dispersal in the USA but not in Argentina. However, Gonçalves da Silva *et al.* (2010) considered that their data were insufficient to confirm the results in Argentina, and therefore recommended additional research. This is a key point, as the observed differences could imply adaptive behavioural changes in the invasive areas, involving features such as dispersal or mating strategies (Gonçalves da Silva *et al.*, 2010).

Here we provide a description of the monk parakeet expansion into the Argentinian Pampas ecoregion in relation to land-use changes during the period 1860–2010. We also compare this process with the monk parakeet invasive expansion into areas of the USA and Europe, and evaluate the significance of our results in terms of current theoretical questions regarding invasion biology.

MATERIALS AND METHODS

The South American Pampas

The South American Pampas was originally a grassland biome that covered eastern Argentina, most of Uruguay, and the southernmost Brazilian state of Rio Grande do Sul. The region is a flat, uniform plain, with the exception of two low-elevation ranges in the province of Buenos Aires: the Tandil and Ventana hills (Fig. 1). In general, soils are deep and very fertile. The climate is temperate, with annual rainfall reaching 1000 mm in the north-east and decreasing to 500 mm in the south-west, and with annual mean temperatures ranging from about 20 °C in the north to 14 °C in the south.

The pre-European Pampas vegetation was a treeless, homogeneous grassland, with shrubs occurring on stony hillocks in the central mountains of Tandil and Ventana. Grassland composition and height gradually changed from east to west in response to the rainfall gradient. In the east, the Humid Pampas subregion was characterized by medium-height grassland with scattered herbs and shrubs. In the west, the Semi-arid Pampas subregion consisted of lower grasslands with some shrubs on sandy soils (Cabrera & Willink, 1973).

The arboreal vegetation originally present in the Pampas included the subarea located east of the Paraná River, including south of Brazil, Uruguay and the Entre Ríos province in Argentina (Fig. 1), where riverine tree forests were common. In addition, a coastal woodland extended along the Atlantic Ocean on slight elevations. These woodlands, locally known as 'talares', were dominated by tala (*Celtis ehrenbergiana*) and algarrobo or mesquite (*Prosopis alba*) trees (Parodi, 1940; Vervoorst, 1967). The talares extended westwards, usually about 40 km inland from the Atlantic coast, and occasionally up to about 100 km in small patches, mostly along the Salado River (Fig. 1).

Figure 1 Left: original distribution of the monk parakeet (*Myiopsitta monachus*) in South America (dark grey) surrounding the Pampas ecoregion (white). Right: main features of the study area, including political divisions, main rivers, hilly terrain and the Flooding Pampas subregion. Vegetation: Pampas grasslands (white) and woodland (grey). E, Espinal ecoregion; T, talares woodland. The small polygons correspond to the administrative units used to map the range expansion of the monk parakeet (detailed information is given in Appendix S1).
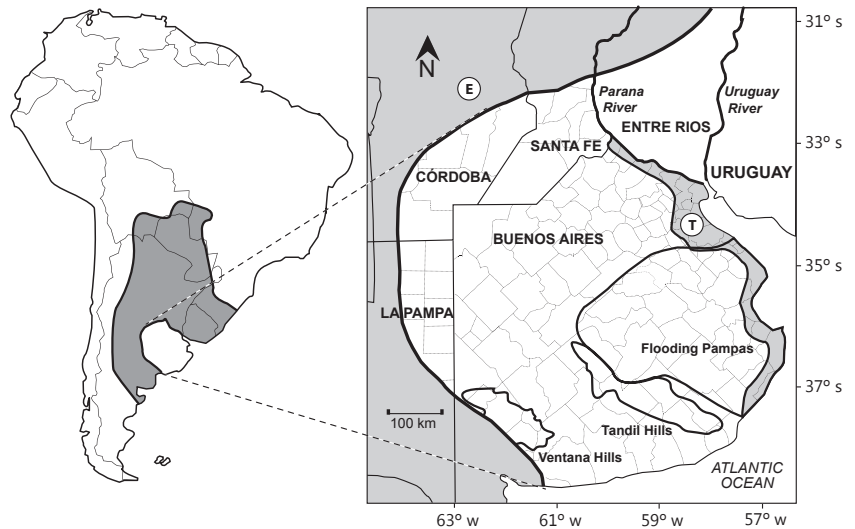
A significant variant of the otherwise uniform Pampas grasslands west of the Paraná River and the talares forest was the vast lowland area (of about 100,000 km²) known as the Flooding Pampas or Salado River basin, located in the south-east of Buenos Aires province (Fig. 1). The very slight slope of the plain leads to extensive and lengthy flooding in years of abundant rainfall, generating a tall tussock grassland as the dominant vegetation (Vervoorst, 1967).

Monk parakeet subspecies

Two subspecies were described originally for the Pampas ecoregion: *Myiopsitta monachus monachus* in the east, and *Myiopsitta monachus calita* in the west (Forshaw & Cooper, 1989). Because of the range expansion described here, their areas overlap at present. We did not separate possible subspecies in our records because specimens assigned to each subspecies in collections were externally very similar and therefore impossible to distinguish in the field, and, more importantly, their taxonomic status remains unclear considering DNA evidence (Russello *et al.*, 2008).

Information sources and methodology

Mapping of the monk parakeet distribution was based on using provincial administrative districts as units. We selected the following points in time, according to the available information: 1860, 1960, 1980, 1990, 2000 and 2010 (see Appendix S1 in Supporting Information). The original distribution of the monk parakeet and subsequent changes over the period 1860–2010 were assessed using the following information sources: (1) museum specimens, (2) published information, (3) published and unpublished reports from provincial government agencies involved in bird pest control programmes (provinces of Buenos Aires, Santa Fe, Córdoba and La Pampa), (4) letters and personal questionnaires distributed among government agencies, researchers, local municipalities

and land owners, (5) internet public media, and (6) extensive travelling by the authors covering the entire study area.

Our approach had some limitations as well as advantages. Limitations included: (1) data were obtained from several sources and did not correspond to a systematic sampling; (2) the data used were presence–absence data for each unit, and therefore did not correspond to the actual localities of the parakeet/nest sightings; and (3) the resolution of the limits of the ranges occupied by the monk parakeet depended on the variable size of the administrative units used.

Advantages included the following. (1) In most cases, records were based on detection of monk parakeet bulky nests, which are very easy to spot even over long distances. In addition, detection was facilitated by the very loud calls constantly uttered by the monk parakeets around nests. This higher visibility conferred more reliability on information provided by farmers and the general public. (2) The monk parakeet was declared an agricultural pest in 1935; as a result, a monitoring scheme has been implemented since the 1950s that requires annual reports of the pest status in each provincial administrative district. In addition, in some cases farmers were requested to report the presence of the monk parakeet on their properties (Pergolani de Costa, 1953). These reports provided a substantial volume of systematic information on historical changes in the distribution of the monk parakeet, and therefore significantly reduced possible errors resulting from differences in observer effort. In summary, we considered that, despite some limitations, the methodology provided adequate and reliable information on the geographical expansion of the monk parakeet in the Pampas.

The linear range expansion for each decade was estimated as the maximum linear distance between the initial and final distribution borders for each period, including the distance from the border of the Pampas in the case of new foci. In the 2000–2010 period, the remaining unoccupied area was occupied by monk parakeets moving inwards simultaneously from

the whole periphery of the area. Therefore, we assumed that the borders of the occupied area were converging on the centre of the still unoccupied area at the same speed. Accordingly, the expansion rate was estimated as the mean distance from the borders to the centre of the free area. This value was obtained by calculating a central point (the centroid, the arithmetic mean position of all the points in the shape) of the still unoccupied area at the beginning of the period (2000).

RESULTS

Land-use changes in the Pampas during the 1860–2010 period

The European occupation of the Pampas resulted in significant alterations in land use and landscape structure that had a strong influence on the bird fauna (Codesido et al., 2011). Key factors influencing habitat suitability for the monk parakeet were changes in grassland structure, weed (thistle) invasion, eucalyptus plantations, agriculture expansion and urbanization along railways.

Grassland structure

The introduction and rapid expansion of livestock resulted in widespread habitat changes that started in the areas under European control. Combined grazing by cattle and sheep changed the grassland structure from tall to short grasses (Gillispie, 1818; Darwin, 1839). Short grass is a preferred feeding habitat for the monk parakeet, as it provides abundant grass and forb seeds (Wetmore, 1926; Aramburú, 1997). In addition, short grass makes cattle excrement available for the monk parakeet, providing an easy source of seeds (Vignolio & Fernández, 2010).

Thistle invasion

Thistles, a highly preferred food item of the monk parakeet, expanded rapidly into a very large area of the Pampas under grazing by sheep and cattle (Darwin, 1839; Gibson, 1919). Thistles were introduced by Europeans, probably with the first settlement in the Buenos Aires area in 1535 (Darwin, 1839), and expanded from the Buenos Aires area into the Pampas until the end of the 19th century, when these species were controlled after widespread ploughing of the Pampas. However, they continue to be common weeds available to monk parakeets in cultivated fields and alongside roads and railways.

Two species were dominant: artichoke thistle (Cynara cardunculus L.) and milk thistle [Silybum marianum (L.) Gaertner]. Head (1826, pp. 2–3) reported that 'On leaving Buenos Aires, the first of these regions is covered for one hundred and eighty miles with clover and thistles; the second region, which extends for four hundred and fifty miles, produces long grass.' Darwin (1839, p. 119) was also amazed by the magnitude of thistle invasion in areas of the Pampas

where cattle had expanded north of the Salado River (Flooding Pampas; Fig. 1). He concluded that 'Over the undulating plains, where these great beds (of cardoon, Cynara cardunculus) occur, nothing else can now live. Before their introduction, however, the surface must have supported, as in other parts, a rank herbage. I doubt whether any case is on record of an invasion on so grand a scale of one plant over the aborigines. As I have already said, I nowhere saw the cardoon south of the Salado; but it is probable that in proportion as that country becomes inhabited, the cardoon will extend its limits.'

Eucalyptus expansion

Eucalyptus species (particularly Eucalyptus globulus Labill) were introduced in Argentina in 1857 (Cozzo, 1955). From 1870 onwards, eucalyptus became very popular among European settlers as a wind-breaker, shade and protection for farm houses, and later as ornamental species in the newly established towns. By 1920, eucalyptus was widespread and fully grown, becoming a distinctive component of the landscape throughout the entire Pampas region (Cozzo, 1955).

Railway expansion and settlement

The railway system in Argentina started in 1860. By 1900 it had reached 16,500 km in length, and by 1920 the network in the Pampas region was almost complete. Farmhouses and small towns along the railway tracks provided suitable breeding and feeding habitat for monk parakeets, which also used telegraph poles along the tracks as nesting places.

Conversion to cropland

At the end of the 19th century, the aboriginal natives were displaced from the Pampas, and the railway network expanded rapidly, facilitating a massive settlement of European immigrants. From the beginning of the 20th century, the grasslands were turned into cropland at a fast rate (Vervoorst, 1967). By 1914, most of the land had been cultivated with crops or introduced pastures, except those less suitable areas, such as the Flooding Pampas and the semi-arid western transition to the Espinal ecoregion that surrounds the western and northern border of the Pampas (Cabrera & Willink, 1973). In summary, cropland expansion in the Pampas underwent three well-defined periods: (1) an initial expansion (1888–1914), (2) a stable period (1914–1970), and (3) a recent expansion (1970–2005) (Fig. 2) (Viglizzo et al., 1997; Reca, 2006).

Range expansion of the monk parakeet in the 1860–2010 period

1860–1960

This period can be subdivided into two subperiods. The first one (1860–1900) was characterized by strong evidence indi-

Figure 2 Changes in the area under agriculture in the Pampas ecoregion, Argentina, during 1888–2005 (data from Reca, 2006).

cating that the distribution range of the monk parakeet remained unchanged. The second subperiod (1900–1960) showed the start of the expansion process into the treeless Pampas. Details are given in the following sections.

Original distribution (1860–1900). The monk parakeet was not present in the Argentine portion of the Pampas, except east of the Paraná River, including the Entre Ríos province in Argentina, and the Uruguayan and Brazilian sectors. This subregion was characterized by the presence of arboreal vegetation along the frequent watercourses, where monk parakeets nested (Darwin, 1839). The monk parakeet was also present in the Paraná River gallery forests down to La Plata River, and further south in the talares forest along the Atlantic Ocean coast, where the monk parakeet nested in tala and algarrobo (mesquite) trees (Fig. 1) (Gibson, 1919; Wetmore, 1926; Pereyra, 1937).

The monk parakeet was absent in the remaining Pampas grasslands west of the Paraná River (the provinces of Buenos Aires, Santa Fe, Córdoba and La Pampa), including the low Tandil and Ventana hills (Figs 1 & 3). Evidence for this period comes from British travellers (Gillispie, 1818; Darwin, 1839; Gibson, 1879) and from a report by scientists from the Argentine National Academy of Sciences, who participated in the military campaign that occupied the native American territory in 1879, travelling extensively across the Pampas grasslands (Doering & Lorentz, 1939). This situation remained stable until about 1900, when the monk parakeet started to expand into the Pampas.

The start of range expansion (1900–1960). There were clear indications that the static original range started spreading across the Pampas grasslands at the beginning of the 20th century. This expansion occurred when the monk parakeet started to nest massively in the eucalyptus trees planted since 1872 by the European settlers (Gibson, 1919). By this time, eucalyptus had reached about 30 m in height, a height preferred by monk parakeets (Volpe & Aramburú, 2011).

According to Ernest Gibson, a naturalist and ranch owner who lived near the talares forest in eastern Buenos Aires province, when he arrived in the area in 1872 the monk parakeet nested solely in the tala trees. At that time, there were three 1-year-old eucalyptus trees in the garden, the first ones grown in the district. These showed such rapid growth and adaptability that from the year 1880 many hundreds were subsequently planted, forming woods, groups and avenues. In 20 years or more, many of these trees attained a height of about 30 m, and the monk parakeets started to nest in eucalyptus 'to the total abandonment of the tala woods' (Gibson, 1919, p. 504). This change in nesting tree preference expanded rapidly in the region (Gibson, 1919; Daguerre, 1936). The preference of monk parakeets for eucalyptus as a nesting tree in the Pampas is still evident today (Table 1).

The transition from native trees to eucalyptus as the preferred nesting tree was probably favoured by the gradual ecotone between the coastal talares woodland and the Flooding Pampas grasslands, with abundant, isolated native forest patches intermingled with eucalyptus plantations (Vervoorst, 1967). This ecotone area expanded westwards during the 1960s, as a result of bird-mediated dispersal of tala and algarrobo trees associated with new perching sites, such as fence posts, windmills and, in particular, eucalyptus plantations (Vervoorst, 1967; Chimento et al., 2012).

Table 1 Proportion (%) of monk parakeet (*Myiopsitta monachus*) nests on different platforms in three localities of Argentina.

Platform	Locality (province)		
	San Cristóbal* (Santa Fe)	General Madariaga† (Buenos Aires)	General Villegas‡ (Buenos Aires)
Eucalyptus (*Eucalyptus* spp.)	75	70	90
Brazilian pine (*Araucaria angustifolia*)		14	2
Pine (*Pinus* spp.) and Australian pine (*Casuarina* sp.)		10	
Tala (*Celtis ehrenberghiana*)		4	
Algarrobo (*Prosopis alba*)	9		
Palm trees (generic)			4
Other trees	7	2	
Artificial structures	9		5
Sample size	2554	–	279

*De la Peña (2000); †Ministerio de Asuntos Agrarios de la Provincia de Buenos Aires (1971); ‡E.H. Bucher, pers. obs.

Another factor contributing to the rapid expansion of the monk parakeet was the new human settlements (farmhouses and small towns) established along the railway network, which became stepping-stones for the dispersion of monk parakeets into the Pampas (Gibson, 1879, 1919; Daguerre, 1936). Nearly all these human settlements had eucalyptus plantations around the houses, as well as fruit orchards that were fed upon by the monk parakeet (Gibson, 1879, 1919; Daguerre, 1936). Moreover, the railway network provided suitable nesting sites in the telegraph posts along the tracks, which were used by the monk parakeet in treeless areas (Bucher & Martin, 1987).

Based on the 1960 distribution map (Fig. 3), the monk parakeet expansive period started from three independent foci: in the south-east, south-west and north-east borders of the Pampas grasslands. The south-east focus originated in the ecotone between the talares woodland and the Pampas grasslands, and expanded rapidly into the Flooding Pampas ecoregion, whereas the other two made little progress and remained stable for a long period (Fig. 3).

1960–1980

The south-east focus continued to expand westwards, still within the Flooding Pampas subregion. The north-east focus expanded moderately to the south, whereas the south-west focus remained unchanged (Fig. 3). Land use in the period showed a moderate increase in the cultivated area of the Pampas (Fig. 2).

1980–1990

A substantial expansion of the south-east focus beyond the Flooding Pampas subregion, together with expansion of the initial foci, led to a coalescence of the area occupied by the monk parakeet in the Pampas. The most significant gain came from the south-east and south-west initial foci (Fig. 3). Land use in the period was characterized by a marked growth in the area under agriculture use (a recent expansion phase; Fig. 2).

Cultivated grains soon became a dominant food item in the diet of monk parakeets, particularly corn, sunflower and, later, sorghum, together with associated weed seeds (Gibson, 1919; Aramburú, 1997). Another cultivated plant food resource resulting from human settlement was fruit trees (particularly peach), planted around farmhouses and later in the new towns that built up alongside railways (Gillispie, 1818; Gibson, 1919). In contrast, bird feeders, a potential food source for monk parakeets, were not used in the Pampas during the study period.

1990–2000

The fast expansion rate of the south-west focus continued during this period (Fig. 3). In addition, a new focus developed in the semi-arid western border of the Pampas. During this period, the area underwent a massive shift in land use, from pastureland to cropland, resulting from a sustained increase in rainfall that had started in the previous decade (Viglizzo *et al.*, 1997).

2000–2010

During this period the monk parakeet finally expanded into the remaining free areas in the Pampas (Fig. 3). Agriculture expansion continued at a high rate (Fig. 2), particularly in the western portion of the Pampas.

Expansion rate

The monk parakeet occupied 327,958 km^2 (about the size of Germany) in about 150 years (1860–2010). However, the effective expansion time may be reduced to 110 years, as the
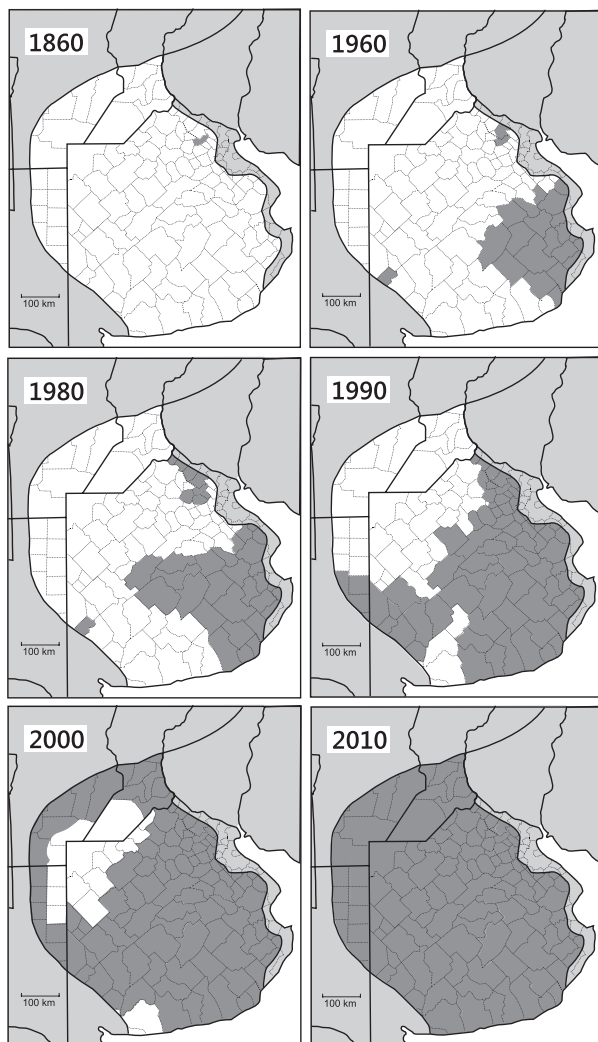

Figure 3 Expansion of the range of the monk parakeet (*Myiopsitta monachus*) in the Pampas ecoregion, Argentina, during 1860–2010. Light grey: area originally occupied by the monk parakeet in 1860. Dark grey: expansion area.

Table 2 Area occupied by the monk parakeet (*Myiopsitta monachus*) in the Pampas ecoregion of Argentina, and average annual linear displacement of the area limits between time periods.

Period	Area (km^2)	Proportion of the Pampas area (%)	Area added (km^2)	Proportion of land added (%)	Linear expansion (km year^{-1})
1860–1900	31,408	8.7	0	0	0
1900–1960	68,189	19.0	36,781	10.2	2.1
1960–1980	122,935	34.2	54,746	15.2	5.6
1980–1990	196,119	54.6	73,184	20.4	6.7
1990–2000	300,973	83.8	104,854	29.2	7.6
2000–2010	359,366	100.0	58,393	16.2	4.0

expansion process only started at the beginning of the 20th century (1900).

According to our data, in all cases the newly occupied districts were contiguous with the already occupied area, indicating that the dispersal followed a neighbourhood diffusion pattern, by which well-established populations act as sources of individuals that disperse short distances into nearby favourable areas (Fig. 3).

The expansion process that started around 1900 was relatively slow and restricted to the Flooding Pampas subregion until approximately 1980, when the monk parakeet spread beyond the Flooding Pampas and occupied the remainder of the Pampas at a faster pace (Fig. 3, Table 2). The annual dispersal rate (from 1900 onwards) ranged between 2.1 and 7.6 km year^{-1}, with the highest values in the 1980–2000 period. The apparent slower expansion rate (in terms of both area and linear distance) observed during the final 2000–2010 period may be an underestimation, because monk parakeets could have occupied the remaining free area in less time (before 2010) without being recorded.

DISCUSSION

Land use and monk parakeet expansion

Expansion of the monk parakeet into the Pampas covered an area close to 330,000 km^2 (about the size of Germany) in the 150 years of the study period, although the effective expansion time may be reduced to 110 years, bearing in mind that the expansion process only started at the beginning of the 20th century. This process was closely related to a sequence of land-use changes introduced by the European settlement, which improved habitat suitability in terms of nesting, feeding and dispersal. For each of these categories, key factors have been detected that help to explain the functional relationship between monk parakeet behavioural rules and the new landscape structure resulting from land-use changes.

Besides land-use changes, we found no indication suggesting that other factors may have influenced the monk parakeet expansion. Climatic factors may be excluded (at least in terms of the bird's physiological tolerance) because the Pampas climate is within the same boundary value ranges of the surrounding Espinal woodlands, where the monk parakeet was originally distributed (Fig. 1).

However, climatic factors may have conditioned the monk parakeet expansion rate indirectly. A long-term increase in the rainfall regime of the Pampas after 1980 and the subsequent changes in land use (Viglizzo *et al.*, 1997) may explain why the monk parakeet expansion was relatively slower and restricted to the Flooding Pampas subregion until around 1980, becoming faster thereafter (Table 2, Fig. 3). The same applies to the south-west expansion focus in the 1980–1990 period, plus an additional eastern focus in the 1990–2000 period (Fig. 3). In all cases, the increase in rainfall led to a shift from pasture to crop production, increasing food availability for the monk parakeet (Viglizzo *et al.*, 1997).

Dispersal in native and invasive sites

Changes in monk parakeet distribution over time indicate that in the Pampas dispersal followed a neighbourhood diffusion pattern, with birds expanding from nearby populations without leaving gaps in between (Fig. 3). This pattern differs from observations of monk parakeet dispersal in Europe and North America, where spread has been faster and more scattered than would be expected via neighbourhood diffusion. Such a difference suggests the predominance of long-range dispersal in Europe (Muñoz & Real, 2006) and North America, where Gonçalves da Silva *et al.* (2010) found genetic evidence of dispersal distances of up to 100 km, one order of magnitude higher than in Argentina.

Possible vagrancy or long-distance dispersal might remain undetected by the method used. However, we consider that this is very unlikely, given the following facts. First, the search effort was significant and relatively homogeneous, thanks to the permanent surveillance by pest control agencies in addition to other sources of information. Second, monk parakeets are easy to detect because of their bulky nests and loud calls (see above). Finally, monk parakeets show a high degree of philopatry, roosting in their compound nests every night throughout the year (Martella & Bucher, 1992; Martin & Bucher, 1993; Eberhard, 1998), and their maximum daily flight range from the nest is about 15 km (E.H.B., unpublished data).

The annual expansion rate found in Argentina (between 2.1 and 7.6 km year^{-1}, depending on the decades; Table 2) was lower than the 10 km year^{-1} value estimated from genetic evidence by Gonçalves da Silva *et al.* (2010) in monk

parakeet populations in Entre Ríos, Argentina, and higher than the natal dispersal distance of about 2 km year^{-1} found in Córdoba, Argentina (Martin & Bucher, 1993). The latter value may underestimate the real dispersal value, given that it corresponds to only 44% of the 186 marked individuals that were recovered from the 600-ha study area, leaving the possibility that some of the unaccounted birds bred further away as part of the long tail of the dispersal distance distribution.

The most plausible explanation for monk parakeet long-distance dispersal in Europe and North America is high propagule pressure resulting from the release (accidental or voluntary) of large numbers of parakeets imported by the pet trade (Muñoz & Real, 2006). Alternative hypotheses to explain long-distance dispersal, such as possible behavioural changes of the monk parakeet in the invasive areas (Gonçalves da Silva et al., 2010), are difficult to disentangle from human-originated releases, as both events might be acting simultaneously.

Key habitat requirements

The expansion of the monk parakeet into the Pampas provides valuable information regarding the species' habitat, including nesting, feeding and landscape requirements.

Nesting

The switch of the monk parakeet to newly available eucalyptus as the preferred nesting platform was a key factor favouring expansion into the Pampas. This exotic tree provided not only a suitable nesting site but also a stepping-stone for dispersal into the treeless grasslands. It is highly probable that dispersal of the monk parakeet would have been at least much slower if the settlers had planted other, less suitable, tree species.

Our study also confirms that monk parakeet nesting preference is not necessarily restricted to specific trees. Instead, the key behavioural rule seems to be selection of the tallest tree or artificial structure available in the landscape, as long as it provides adequate support for the heavy compound nests. Preference for the tallest platforms available has been reported in the native area (Gibson, 1919; Forshaw & Cooper, 1989; Eberhard, 1998; De la Peña, 2000) as well as in invasive sites in Europe and North America. In Spain, this pattern is widespread, including palm trees in Barcelona and Canarias (Sol et al., 1997), eucalyptus in Malaga, cypress and pines in Mallorca, unspecified tall trees in Madrid, and electricity poles in Cartagena (Muñoz & Real, 2006). Preference for the tallest nesting sites has also been found in Florida, USA (Burger & Gochfeld, 2000; Pranty, 2009).

Feeding

Throughout the expansion period, the monk parakeet adapted to exploit a variety of new food sources, including cultivated and wild seeds, fruits, leaf buds, cotyledons of emerging plants and even pollen (Aramburú, 1997). It also adapted to new environments, including pastureland, cropland and human settlements. This marked plasticity was favoured by the ability of monk parakeets to feed on the ground as well as on trees (Wetmore, 1926; Aramburú & Corbalán, 2000).

Landscape structure

Our observations indicate that the ability of the monk parakeet to exploit food resources is spatially restricted by its resident, non-migratory condition, and even more so given its need to roost in the nest daily, even during the non-breeding season. Accordingly, monk parakeets need a minimal landscape area that includes both nesting sites and year-round food availability within a maximum radius of about 15 km from the nest (E.H. Bucher, unpublished data). The need for these fine-grained areas may condition expansion substantially and explain the monk parakeet's preference for urban landscapes instead of coarser grain landscapes such as forests (Strubbe & Matthysen, 2009).

Another consequence of a restricted search area is that the dispersing individuals probably gather information on suitable nesting places during their daily foraging trips. This behaviour would be consistent with the reduced dispersal distance observed in marked individuals (Martin & Bucher, 1993) as well as the neighbourhood diffusion pattern detected in this study.

What makes the monk parakeet a successful invader?

The monk parakeet shows some traits expected in successful invaders, such as lack of a migratory condition and sexual dichromatism, as well as the existence of pre-adaptive invasive conditions, such as inhabiting human-modified habitats and a history of close association with humans in their native range (Duncan et al., 2003).

In contrast, communal breeding, a fixed, single, breeding season, delayed reproduction and short breeding dispersal distance (Navarro et al., 1992; Martin & Bucher, 1993) do not agree with expected traits, such as high population growth rates, opportunistic breeding and nomadic movements, and a rapidly developing species with high fecundity (Duncan et al., 2003). This incomplete correspondence is consistent with growing evidence suggesting that there is no single set of traits that defines successful invasive species (Thuiller et al., 2006; Sol et al., 2012). More importantly, our research suggests that the monk parakeet exhibits other traits that may provide a more general explanation for its success in establishing in new areas, which have been somewhat ignored until now: the ability to build communal nests, behavioural flexibility and dietary opportunism. The ability to build communal nests (instead of depending on cavities in trees or cliffs, as other parrots do) provides the monk parakeet with a significant adaptive advantage for range

expansion. The communal nest provides not only a well-protected breeding site that may be located in a wide variety of sites, but also a year-round roosting site for the whole population (all parakeets spend the night in nests), ensuring protection against predators and ameliorated winter temperatures (Spreyer & Bucher, 1998). The only limiting factor for the bulky nest is the availability of adequate platforms to support its weight, which may exceed 1000 kg (Spreyer & Bucher, 1998).

Parrots, which live in complex social groups and have a long developmental period before becoming independent, have demonstrated ape-like intelligence. Like apes, parrots are highly innovative in their feeding strategies, having demonstrated the ability to process complex covered foods, such as shells, and the tough skins of some fruits (Emery, 2006). Dietary opportunism in parrots is greatly enhanced by their morphological adaptations, including a strong beak and a flexible foot structure. The parrot bill is an extremely versatile tool that allows access to many fruits and seeds, including very hard seeds such as palm fruits. Their peculiar foot structure allows them to hang in the vegetation, and reach and handle food items expertly (Forshaw & Cooper, 1989). Dietary opportunism is evident in the monk parakeet, which can feed on seeds, fruits, leaf buds, cotyledons of emerging plants, pollen and even insects, both in trees and on the ground (Forshaw & Cooper, 1989; Aramburú, 1997). Monk parakeets have also been found to be innovative in exploring new resources, such as grain crops, and in the way they handle protected food sources, for example corn husks, sunflower heads and even bin bags, which they are able to tear open easily (E.H.B., pers. obs.). Thus parakeets are able to gain access to resources that are inaccessible to other birds. Moreover, their complex social life around the communal nest is another indirect indication of high intelligence.

Information from the native range helps to improve species distribution models

Our study provides useful insights in terms of the dynamics of the invasive process that are applicable to other species (Sax et al., 2007). Of particular interest are the following aspects.

1. Equilibrium condition in the native range. Species dispersal models assume that species are in equilibrium with climate/habitat ecological niches in their native range, and therefore ecological niches are long-term stable constraints on the potential geographical distribution of species (Peterson, 2003). However, the spread of the monk parakeet across new areas close to its historical range is a clear demonstration of a non-equilibrium situation within the native range.

2. Selection and analysis of predictor parameters. Information on the key habitat requirements of the monk parakeet in its native range provides useful insights for a more effective selection of prediction parameters. For example, the 'presence of exotic forests' (Strubbe & Matthysen, 2009) could become more predictive if the species composition of

these forests is considered, particularly in terms of preferred nesting trees such as eucalyptus and palms. Moreover, forest cover and habitat suitability for monk parakeets may not follow a simple, linear relationship. Large, uniform forest patches may not be occupied by monk parakeets (Strubbe & Matthysen, 2009) but instead smaller patches may be used extensively as long as they belong to a fine-grained landscape that includes nesting sites and year-round feeding habitat compatible with the search area of the species.

Used retrospectively, information from the species' native site may also help disentangle the functional significance of predictor parameters that are very broad and may refer to large-scale surrogates for one or several direct factors. For example, the preference of monk parakeets for urban areas in invasive sites (Davis et al., 2014) may translate into the availability of nesting habitat (suitable trees or artificial structures) and/or a year-round food supply (bird feeders, rubbish, fruits, etc.).

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 First records of monk parakeet in the Pampas ecoregion of Argentina according to departmental political boundaries.

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