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# Establishment Success across Convergent Mediterranean Ecosystems: an Analysis of Bird Introductions

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**Abstract:** *Concern over the impact of invaders on biodiversity and on the functioning of ecosystems has generated a rising tide of comparative analyses aiming to unveil the factors that shape the success of introduced species across different regions. One limitation of these studies is that they often compare geographically rather than ecologically defined regions. We propose an approach that can help address this limitation: comparison of invasions across convergent ecosystems that share similar climates. We compared avian invasions in five convergent mediterranean climate systems around the globe. Based on a database of 180 introductions representing 121 avian species, we found that the proportion of bird species successfully established was high in all mediterranean systems (more than 40% for all five regions). Species differed in their likelihood to become established, although success was not higher for those originating from mediterranean systems than for those from nonmediterranean regions. Controlling for this taxonomic effect with generalized linear mixed models, species introduced into mediterranean islands did not show higher establishment success than those introduced to the mainland. Susceptibility to avian invaders, however, differed substantially among the different mediterranean regions. The probability that a species will become established was highest in the Mediterranean Basin and lowest in mediterranean Australia and the South African Cape. Our results suggest that many of the birds recently introduced into mediterranean systems, and especially into the Mediterranean Basin, have a high potential to establish self-sustaining populations. This finding has important implications for conservation in these biologically diverse hotspots.*

**Key Words:** biological invasions, birds, convergence, GLMM, introduced species, mediterranean-climate systems

Exitoso de Establecimiento en Ecosistemas Mediterráneos Convergentes: un Análisis de Introducciones de Aves

**Resumen:** *La preocupación por el impacto de las especies invasoras sobre la biodiversidad y el funcionamiento de los ecosistemas ha generado una creciente ola de análisis comparativos que tratan de revelar los factores que moldean el éxito de las especies introducidas en diferentes regiones. Una limitación de esos estudios es que a menudo comparan regiones definidas geográficamente y no ecológicamente. Proponemos un método que puede ayudar a superar esa limitación: la comparación de invasiones en ecosistemas convergentes que comparten climas similares. Comparamos las invasiones de aves en cinco sistemas climáticos mediterráneos alrededor del mundo. A partir de una base de datos de 180 introducciones representando a 121 especies de aves, encontramos que la proporción de especies de aves que se establecieron exitosamente fue alta en todos los sistemas mediterráneos (más de 40% en las cinco regiones). Las especies difirieron en la probabilidad de establecimiento, aunque el éxito no fue mayor para aquellas que se originaron en sistemas mediterráneos en comparación con las provenientes de regiones no mediterráneas. Controlando este efecto*

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*taxonómico con modelos generalizados lineales mixtos, las especies introducidas en islas mediterráneas no mostraron mayor éxito de establecimiento que las introducidas en tierra firme. Sin embargo, la susceptibilidad a invasores aviarios difirió sustancialmente en las diferentes regiones mediterráneas. La probabilidad de establecimiento de una especie fue mayor en la Cuenca Mediterránea y menor en Australia y África del Sur. Nuestros resultados sugieren que muchas de las aves introducidas a los sistemas mediterráneos recientemente, especialmente en la Cuenca Mediterránea, tienen un alto potencial para el establecimiento de poblaciones autosostenibles. Este hallazgo tiene implicaciones importantes para la conservación en estas regiones biológicamente diversas.*

**Palabras Clave:** aves, convergencia, especies introducidas, GLMM, invasiones biológicas, sistemas climáticos mediterráneos

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## Introduction

Invasions of communities by nonindigenous species pose a major threat to the maintenance of native biodiversity and impose substantial economic and health costs to human societies (Wilcove et al. 1998; Lockwood et al. 2000; D'Antonio & Kark 2002). Consequently, it is crucial to quantify and better understand introduction and establishment patterns. Past comparative studies based on historical records of introductions have significantly improved our understanding of the ecology of biological invasions (Rejmánek 1989; Duncan et al. 2003). Progress has been particularly notable for birds (Duncan et al. 2003), for which good historical records of successful and failed introductions to various locations around the world exist (e.g., Long 1981; Lever 1987). The study of these introductions has allowed identification of some of the factors that influence the successful transition from introduction to establishment (reviewed in Duncan et al. 2003).

Despite this progress, two drawbacks to using historical introductions to investigate the invasion process, we believe, have been underappreciated in earlier studies. First, attempts to analyze introduction data may be complicated by the fact that the different regions examined may have very different climatic and ecosystem characteristics. For example, large-scale analyses tend to show that more diverse systems contain higher numbers of exotic species (Shea & Chesson 2002), an observation that is contrary to theory (Elton 1958). This discrepancy, however, may be explained if extrinsic factors that vary at these spatial scales favor high numbers of native species and increase niche opportunities for invaders. A second limitation is that the scale of study has often been defined based on geographical criteria (e.g., country) rather than on ecological similarity. For example, some studies pool all introductions into large, countrywide regions (e.g., United States, Australia), although it seems clear that ecological differences within such large regions may in some cases be larger than among regions. These limitations may have masked patterns that are important for better understanding the process of invasion.

Here, we propose that a comparative study of convergent ecosystems can provide a valuable, complementary framework to address these issues. Such an approach enables one to investigate patterns and processes that affect the success and failure of species introductions while adjusting for fundamental climate region and ecosystem-type differences. We applied such a framework to studying avian invasion patterns across the Mediterranean climate systems: the Mediterranean Sea Basin, central California, the South African Cape, central Chile, and southern and southwestern Australia. All Mediterranean climate systems share similar global atmospheric and oceanic circulation patterns, most of them occurring on the western shores of continents (Hobbs et al. 1995). They occur between latitudes 30° and 42° in both northern and southern hemispheres and are characteristically biseasonal (i.e., dry summers with no rain and mild rainy winters; di Castri 1991; Hobbs et al. 1995). Although widely separated geographically, these regions share many climatic and ecological similarities (di Castri 1991; Hobbs et al. 1995), and many of their animal and plant species have undergone convergent evolution (Johnson 1973). Mediterranean climate systems provide a particularly useful model system for comparing the response of convergent ecosystems to invasion (di Castri & Mooney 1973). First, substantial ecological and historical research has been done in each of the Mediterranean climate regions (e.g., di Castri 1989, 1991; Hobbs et al. 1995), providing excellent information for comparative analyses. Second, all five of these systems are included among Earth's 25 biologically most diverse and endemic biodiversity hotspots that are at risk (Médail & Quézel 1999; Myers et al. 2000) and in the global list of ecoregions that warrant special conservation attention (Olson & Dinerstein 1998). Thus, examining the invasion process in Mediterranean climate systems is particularly timely to help prevent and mitigate potential threats of invaders to the native biodiversity of these regions.

For a species to become established in a novel region, it needs to find an appropriate niche (Shea & Chesson 2002). The likelihood of finding an appropriate niche depends in turn on the invasion potential of the species, the

characteristics of the region of introduction, and the ecological similitude between the native and novel regions (Duncan et al. 2003). We used the patterns of historical introductions into convergent mediterranean ecosystems to assess the importance of these three factors on establishment success. Specifically, we asked three major questions: (1) Are all mediterranean climate regions similar in the patterns of establishment of species or are some regions more susceptible to invaders than others? (2) Do species (or higher taxonomic groups) differ in their ability to establish themselves in the non-native regions? (3) Do species originating from mediterranean climate systems have higher chances to establish themselves in other mediterranean climate systems than species from different (nonmediterranean climate) regions? We examined these questions with novel statistical techniques that effectively dealt with the problems of clustering and non-independence of the data that characterize human-driven introductions (Blackburn & Duncan 2001a, 2001b).

## Methods

### Introduction Data

Information on introductions, collected by S.K., was first compiled from Long (1981) and Lever (1987). These two sources alone do not include all known introduction attempts for the different regions studied, both successful and failed. In addition, in some cases the introduction outcome based on these sources was unclear or was not updated. Therefore, we updated and confirmed this information with more specific regional and local literature. The sources we used include published books and papers (main sources: Cramp & Simmons 1980; Rolls 1984; Paz 1987; Batllori & Uribe 1988; Root 1988; Hengeveld 1989; Higgins 1990; Marchant & Davies 1990; Marchant & Higgins 1990; Blondel 1991; Vuilleumier 1991; Macdonald 1992; Smallwood 1994; Price et al. 1995; Saunders & Ingram 1995; Higgins & Davies 1996; Munoz-Pedreras et al. 1996; Porter et al. 1996; Reino & Silva 1996; Shirihai 1996; Simpson & Day 1996; Hagemeyer & Blair 1997; Harrison et al. 1997; Garrett 1997; Leishman 1997; Shoham et al. 1997; Sol et al. 1997; Koenig 1998; Snow & Perrins 1998; Olsen 2000; Vilà et al. 2001; Sapir 2003), published and unpublished bird atlas projects (e.g., for Australia and South Africa), published bird guides, published reports, usually at a country or regional scale (e.g., Andreotti et al. 2001), unpublished reports (e.g., Australia, Olsen 2000; Israel, Hatzofe 2003), and bird checklists for countries (available on official country Web pages or sent to us directly). Finally, we verified all the data with experts in all five regions (see Acknowledgments).

We confirmed that only introductions that occurred in regions with "real" mediterranean climates (*sensu* Hobbs et al. 1995) were included in our database. For

example, although much of Spain and Portugal have a mediterranean climate, in their northern parts the climate is continental and therefore we excluded introductions into these nonmediterranean areas. We focused on terrestrial and freshwater birds. Few introductions of seabirds have been documented (Long 1981). We did not include natural colonization by range expansion (i.e., species that arrived alone from their native or non-native distribution) or reintroductions into former native habitat. We included, however, cases where the species was introduced outside its native range but within the same mediterranean-climate region (e.g., introductions from southern Australia [native range] to Kangaroo Island [non-native range]). We excluded introduction events in which only one individual was known to be introduced or cases of hybrids between native and non-native subspecies (such as Japanese Quail [*Coturnix japonica*], which was unsuccessfully introduced in Italy but generated hybrids with native quail). Finally, species for which there were doubts whether the introduction was originally into a mediterranean-climate region (e.g., in cases where records only state the species was introduced into, for example, Italy) were also excluded.

An introduction was considered successful when the species established a breeding population in the non-native region. Although we collated all records that applied to the guidelines mentioned above, we included only species that were introduced before 1990 in the analysis of establishment success. Data on more recent introductions were not included because it may be too early to determine whether these species are currently establishing a viable breeding population. These data were recorded, however, and are available from <http://shum.huji.ac.il/~salit/>. To examine establishment success, we removed the eight introductions from Chile because the quality of the information available, especially for failed introductions, was poor and could bias the results.

### Statistical Analysis

Nonrandomness in introduction patterns among regions and families was assessed using contingency tables (Blackburn & Duncan 2001b; Cassey et al. 2004). We examined differences in establishment success among regions and between species by modeling the relationship between the response variable (success or failure of introduction) and each of the following explanatory variables: (1) region of introduction (coded as Mediterranean Basin, Australia, California, and Cape; Chile was excluded); (2) taxonomic group (species and family levels, following Sibley & Monroe 1990); and (3) type of region of origin of the introduced species (coded as mediterranean vs. non-mediterranean climate region).

In general, studies of establishment success present two major statistical difficulties (Blackburn & Duncan 2001a; Duncan et al. 2003). First, species cannot be

treated as independent data points because closely related species may share some attributes, due to common ancestry, that can influence their chances to establish themselves in new regions. Second, patterns of success may be biased because species were not randomly distributed among introduction locations and because some locations received disproportionately more invaders or a larger proportion of better (or poorer) invaders than other regions. Following Blackburn and Duncan (2001*a*), we dealt with these problems by means of generalized linear mixed modeling (GLMM, Littell et al. 1996). We used the GLIMMIX macro in SAS to model the outcome of the introduction (Littell et al. 1996), including variables that coded for the clustering of introduction events within species and higher taxa as random effects. We specified a variance component model with a different intercept for each species and family but used the same slopes (Blackburn & Duncan 2001*a*). The rest of the explanatory variables (region of introduction and region of origin of the introduced species) and other potentially confounding variables (see below) were coded as fixed factors. Introduction success is a binomial variable; that is, it can adopt only one of two values: success or failure. We therefore defined our model with a binomial error and a logit link (Littell et al. 1996). First-order interactions between factors were tested, but none was significant in the model.

We controlled for two potential biases in the GLMM models. First, establishment success may be enhanced in cases of introductions that occur within the same mediterranean-climate region, even when these areas are outside the natural distribution of the species. We therefore included in the model a fixed factor that coded for whether or not the introduction was within the same mediterranean-climate region. Second, introductions on islands are often assumed to have a better probability to succeed than introductions on continents, although evidence to date does not support this hypothesis in birds (Sol 2000; Blackburn & Duncan 2001*b*). As a precaution, however, we considered whether the introduction was on an island or on the mainland as a fixed factor. In total, after excluding Chile because of small sample size, we included in the model 155 introductions of species before 1990 and 17 additional introductions between 1990 and 2002.

Another potential source of bias in our dataset results from the fact that information on the number of times each species was introduced and the number of individuals released or escaped was not available for most introductions. We reduced the effect of this lack of information by controlling for taxonomy in the mixed model. This ensured that the significance of the tests for the fixed-effect predictors was not biased by unmeasured traits (such as introduction effort) shared at the species and family levels (Duncan et al. 2001; Cassey et al. 2004). In addition, we tested our explanatory variables after adjusting for the effect of introduction mode in the model. Deliberate in-

troductions generally involve a higher introduction effort than accidental introductions (D.S., unpublished). If introduction effort had a major effect on the patterns of success and failure seen across the different mediterranean-climate systems, we would expect deliberate and accidental introductions to differ in the patterns they show.

### Explaining Patterns of Species Establishment among Regions

To better interpret variation in patterns of species establishment among regions, we quantified the area size, the species richness of native breeding birds (number of species), and the levels of human impact for each of the regions studied (Table 1). Information on area size, measured in thousands of square kilometers, was based on World Wildlife Fund (WWF) ecoregions (Olson et al. 2001) (<http://www.worldwildlife.org/science/data/terreco.cfm>) and was calculated in ArcView 3 after applying an equal-area projection. Richness estimations were based on Vuilleumier (1991), Blondel and Aronson (1999), and W. R. J. Dean (unpublished). For the mediterranean regions of Australia, the figure was calculated for the purposes of this paper based on Higgins (1990), Marchant and Davies (1990), Marchant and Higgins (1990), Saunders and Ingram (1995), Higgins and Davies (1996), and Simpson and Day (1996).

Human impact was estimated based on the Global Human Footprint data set (Sanderson et al. 2002). It provides an index of human influence (HII) normalized by biome and realm. The HII is based on a global data set of 1-km grid cells created from nine global data layers covering human population pressure (population density population settlements), human land use and infrastructure (built-up areas, nighttime lights, land use, and land cover), and human access (coastlines, roads, railroads, navigable rivers). Although the time period for the data is between 1992 and 1995, it represents the outcome of decades of human-related disturbance. We downloaded HII data and used ENVI 3.5 (Research Systems 2001) to calculate the mean HII for each of the mediterranean ecoregions, as identified on the WWF ecoregion map layers (Olson & Dinerstein 2002).

## Results

### Introduction Patterns

We found 180 introductions into mediterranean-climate systems of 121 species (list of species available from <http://shum.huji.ac.il/~salit>). Of these, 162 introductions belonging to 105 species and 18 families occurred before 1990. The species introduced were a nonrandom sample of all extant avian species ( $\chi^2 = 256.34$ ,  $df = 18$ ,  $p < 0.0001$ ), with six avian families accounting for 78% of all introductions. Families were nonrandomly distributed

**Table 1.** Total number and percentage of successful bird introductions in each of the five mediterranean climate systems in our database.

Region	Total species introduced	Species introduced before 1990	Successful introductions (%) <sup>a</sup>	Families introduced <sup>a</sup>	Native breeding bird species	Area (× 1000 km <sup>2</sup> )	Human impact index (SD) <sup>b</sup>
California	44	42	69	13	172	121	25.7 (18.0)
Mediterranean Basin	42	26	100	7	347	2316	29.1 (11.9)
Australia	63	63	49	16	267	773	14.2 (10.5)
Cape	24	24	42	10	316	76	26.4 (13.1)
Chile	8	7	100	6	121	141	22.9 (13.0)

<sup>a</sup>Calculated based only on the introductions that occurred before 1990.

<sup>b</sup>See text for details on index.

with respect to the mediterranean region of introduction as well ( $\chi^2 = 92.92$ ,  $df = 72$ ,  $p = 0.049$ ). For example, Passeridae were introduced mainly in the Mediterranean Basin, Columbidae mainly in Australia, and Psittacidae mainly in California.

Several other nonrandom patterns deserve attention. First, introductions to islands were not randomly distributed among the different mediterranean systems ( $\chi^2 = 15.29$ ,  $df = 4$ ,  $p = 0.004$ ). For example, introductions to islands (primarily Kangaroo Island) were more frequent in Australia than in other regions. Second, different mediterranean systems also differed in the mode of introduction ( $\chi^2 = 18.41$ ,  $df = 4$ ,  $p = 0.001$ ). In Australia deliberate introductions were more frequent than in California and the Mediterranean Basin. Third, there were relatively few introductions of species within the same mediterranean-climate region into an area that was not part of their native range, and most of them (13 out of 19 introductions) occurred in Australia. Finally, Australia also received significantly more introductions of species native to other mediterranean systems than did California and the Mediterranean Basin ( $\chi^2 = 14.23$ ,  $df = 4$ ,  $p = 0.006$ ).

### Establishment Success

Introduction success was high in all mediterranean-climate systems. Overall, 64% of all known introductions were successful when analyzed for all mediterranean-climate regions pooled (binomial test,  $p = 0.0002$ ). There was, however, substantial variation in establishment success among the different regions, ranging from 42% in the Cape to 100% in the Mediterranean Basin and Chile (Table 1). The region of introduction significantly affected the probability of establishment when phylogenetic autocorrelation and confounding effects were accounted using the GLMM approach (Table 2). The probability of establishment was higher in the Mediterranean Basin than in California. The latter was higher than that of both Australia and Cape, which did not differ from each other. The GLMM model also revealed that the probability of establishment varies significantly among species but not among families. When testing for the effect of introduction mode, we found no significant differences between deliberately and accidentally introduced groups. None of the other variables was significant in the model (Table 2).

**Table 2.** Fixed-effect and random-effect parameters of a generalized linear mixed model (GLMM) of the variation in establishment success for bird species introduced in four mediterranean climate systems.

Factor	Categories	Estimate	SE	t <sub>47</sub>	p	
Fixed	region of introduction	Mediterranean Basin	4.890	1.161	4.21	0.0001
		California	1.496	0.616	2.43	0.0190
		Australia	0.385	0.531	0.72	0.4722
		Cape	0.000	.	.	.
	same mediterranean region*		1.541	1.022	1.51	0.1384
	species of mediterranean origin		-0.895	0.670	-1.34	0.1883
	mode of introduction	deliberate	-1.205	0.866	-1.39	0.1707
		accidental	-0.314	0.686	-0.46	0.6494
		unknown	0.000	.	.	.
	introduction to an island		1.432	0.804	1.78	0.0815
Random	ratio			Z		
	family	1.9044	0.882	0.901	0.98	0.1637
	species (family)	9.1128	4.220	1.250	3.38	0.0004

\*Species introduced into the same mediterranean climate region of the four regions included.

## Discussion

Our analysis of bird introductions across the five convergent mediterranean-climate regions shows interesting similarities and differences in the patterns of introduction among the systems. This informs us about the role of community invasibility in determining establishment success of invaders.

In most mediterranean-climate systems, the quantity of species introduced was relatively high, and the number of species that have become established was high relative to those that have failed. This high introduction success is remarkable, given that it is generally assumed that only a small proportion of the species introduced will successfully establish sustained breeding populations (e.g., Lodge 1993). For example, Williamson and Fitter (1996) proposed the "Tens Rule," which suggests that only about 10% of introduction attempts are expected to be successful. Obviously, the record of failed introductions is likely to be less complete than that of successful introductions because species that failed to establish leave no further trace of their presence. This alone, however, is unlikely to explain the high establishment success in the different mediterranean-climate systems because these regions are among the best studied in the world. In addition, introduction mode did not affect its fate. This suggests that the probability of detecting failures in accidental introductions is not different from that found in deliberate introductions, where failures are recorded more reliably.

Despite the generally high establishment success, the five mediterranean-climate systems showed substantial differences in their susceptibility to invaders. The probability that a species would establish was highest in the Mediterranean Basin, intermediate in California, and lowest in Australia and the Cape systems. These results challenge the widely held perception that the Mediterranean Basin is more resistant to invasion than other mediterranean-climate systems (Blondel & Aronson 1999). One reason behind this perception is that the Mediterranean Basin has been prone to high human-related impacts over thousands of years; this process may have led to higher resistance to new invasions (Blondel & Aronson 1999).

Although this hypothesis has not been quantitatively examined before, it has led to an underestimation of the ecological and economic importance of invaders in the Mediterranean Basin, especially when compared with most other mediterranean regions in which invasion is considered a major conservation problem. Yet, in recent years the number of new introductions reported in both the western (e.g., Costa & Schaffer 2000; Andreotti et al. 2001) and the eastern Mediterranean Basin (e.g., Mendelsohn & Yom-Tov 1999; Hatzofe & Yom-Tov 2002) has increased dramatically. If our results reflect a general pattern, many of these introduced species have a great

potential to succeed and establish self-sustaining populations. This may enhance the current biotic homogenization (Lockwood et al. 2000) and may have detrimental impacts on native species (e.g., direct predation, competition for food or transfer of disease; Lever 1994; Ebenhard 1988) and on human societies (e.g., damage to agriculture; Lever 1994; Ebenhard 1988). Thus, there is an urgent need to further investigate the invasion process of birds introduced in these regions, and especially in the Mediterranean Basin.

Why do mediterranean-climate systems differ in their probability of being successfully invaded? There are several possible explanations, which should be further tested empirically in future studies. First, establishment success may vary among regions if introduction effort has been higher in some regions compared with others. Differences in introduction effort do not, however, seem to explain the major differences in invasibility among mediterranean climatic regions. It appears that birds introduced to Europe, in which much of the Mediterranean Basin exists, have actually been released in smaller (rather than larger) numbers than those introduced to Australia, the United States, Africa, or South America (Cassey et al. 2004).

Second, patterns of success may be biased if species are not randomly distributed among introduction locations. Such bias could appear if, for example, certain locations receive a disproportionately higher number of better (or poorer) invaders than others. Indeed, different species in our database showed differences in their ability to invade different systems, and species were nonrandomly distributed among the regions. This is consistent with previous findings (Blackburn & Duncan 2001a, 2001b; Sol et al. 2002) and suggests that establishment success may depend largely on the properties of the invader. Interestingly, species that originate in mediterranean systems are not more successful than those originating from other climatic systems, suggesting that rather than specific adaptations to mediterranean-climate systems, invasion success is mainly affected by some general characteristics of the species (reviewed in Duncan et al. 2003). The conclusion that some regions are more susceptible to invaders remains, however, when we statistically control for this taxonomic effect by applying the GLMM approach. This suggests that species-level effects are insufficient to explain the differences in susceptibility to invaders among mediterranean-climate systems.

A third possibility is that mediterranean-climate systems differ in their invasibility to alien birds (Lonsdale 2001). Ecological theory offers two main classes of explanations for variation in community resistance: biotic resistance and ecological disturbance. The biotic resistance hypothesis proposes that strong biotic interactions of aliens and natives will hinder the establishment and spread of introduced species, leading to their failure to

invade native communities (Elton 1958). This hypothesis predicts that establishment success should be lower in species-rich communities, where an invader has a higher chance to encounter a competitor, predator, or parasite that would prevent its population growth and expansion. Although biotic resistance has long been accepted as a major factor shaping introduction outcome, it has received mixed empirical support in plants (Levine & D'Antonio 1999) and is not supported in birds. For example, Case (1996) found that the number of established bird species did not vary significantly with the native avifauna richness. In addition, birds do not seem to invade islands more easily than the mainland (Sol 2000; Blackburn & Duncan 2001*b*), even though islands are more impoverished in species (Vitousek 1988). We did not manage to detect differences between islands and the mainland in establishment success, despite comparing regions with similar climatic conditions and thus at least partly controlling for this factor.

The disturbance hypothesis, on the other hand, predicts that establishment should be favored in communities that have been prone to higher levels of disturbance, especially human-related disturbances. Human activities can create novel niches by generating new resource opportunities, enemy reduction, or expansion of existing niches, providing new opportunities for invaders (Mack et al. 2000; Shea & Chesson 2002). The disturbance hypothesis has not been properly tested in birds, although the fact that most exotic birds establish in habitats highly modified by humans (Case 1996), such as urban and agricultural areas, lends some credibility to this possibility. With the exception of the Cape region, our results support this hypothesis. Mediterranean-climate systems showed a partial pattern of increasing invasibility as a function of disturbance (Table 1). The Mediterranean Basin, which had the highest establishment success, also had the highest levels of human impact. Although sample size was admittedly small, it seems reasonable to tentatively attribute part of the differences between regions to differences in disturbance levels, recognizing at the same time that biotic resistance may also be an important actor in highly diverse ecosystems. This would explain, for example, why the Cape, which is a very diverse region, shows lower invasibility than would be expected according to its relatively high level of human-related disturbance. A combination of factors is most likely shaping the patterns of establishment success uncovered in this study.

To conclude, our analysis of convergent ecosystems provides support for the hypotheses that establishment success is affected by both the invasion potential of the introduced species and the characteristics of the region of introduction. We believe our approach, which takes into account climatic and ecological differences among regions, demonstrates the utility of comparing invasion patterns across convergent ecosystems. A similar approach can be applied to other taxonomic groups such as plants

and mammals and to other convergent systems (e.g., boreal and grassland). Such an approach can significantly contribute to our understanding of invasion processes and enhance our ability to predict and prevent the detrimental effects of alien species on natural ecosystems.

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