Chapter 5
Why Are Exotic Birds So Successful in Urbanized Environments?

Daniel Sol, Cesar González-Lagos, Oriol Lapiedra, and Mario Díaz

Abstract Many nonindigenous organisms, including birds, are often restricted to human-altered environments within the region of introduction. The classical explanation is that human-related alterations make the environment easier to invade by reducing biotic resistance and offering new niche opportunities. However, the pattern may also reflect that many more species have been introduced in human-altered environments and/or that traits associated with invasion success and the ability to thrive in these environments are related. In this chapter, we argue that if we want to fully understand why exotic organisms are mainly successful in human-altered environments, we need to see the invasion process as a set of stages with different probabilities of being transited. Applied to birds, this framework suggests that there is a high probability that an exotic species ends up associated with human-altered environments if the species: (1) is more abundant (and hence more available for introduction) in urbanized environments; (2) has a higher chance to be successfully transported, as it is already habituated to humans; and (3) has a higher probability to be introduced in an urbanized environment, where most humans live. If these arguments are true, then the exotic species is

D. Sol (✉)
CREAF (Centre for Ecological Research and Forestry Applications), Barcelona, Espanya, Spain

CSIC (Spanish National Research Council), Bellaterra, Catalonia 08193, Spain
e-mail: d.sol@creaf.uab.es; dsolrueda@gmail.com

C. González-Lagos
Departamento de Ecología, Facultad de Ciencias Biológicas, Pontificia Universidad Católica de Chile, Santiago, Chile

Center of Applied Ecology and Sustainability (CAPES), Pontificia Universidad Católica de Chile, Santiago, Chile
e-mail: cesar.glagos@gmail.com

O. Lapiedra
Department of Biological Sciences, University of Rhode Island, Kingston, RI, USA
e-mail: o.lapiedra@gmail.com

M. Díaz
Department of Biogeography and Global Change (BGC-MNCN-CSIC), National Museum of Natural Sciences, CSIC, c/Serrano 155bis, 28006 Madrid, Spain
e-mail: Mario.Diaz@ccma.csic.es

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likely to successfully establish itself in the new region because the species should already have the traits needed to persist in the novel environment. Although more supporting evidence is needed, the proposed framework provides a general solution for the paradox that many invaders are more successful in the new environment than most native species.

Keywords Biological invasions • Invasion success • Biotic resistance • Novel niches • Life history • Anthropocene

5.1 Introduction

Ever since Elton (1958), environmental disturbances are deemed essential to understanding invasion success. This is reflected in the higher success of invaders in altered environments than in more pristine ones (Sax and Brown 2000). Birds fit well to this pattern; not only they tend to be more frequent and abundant in such environments, notably urbanized environments, but many seem to be unable to expand to more pristine habitats (Case 1996; Fig. 5.1). Diamond and Veitch (1981) first noted this in New Zealand, where alien birds are highly abundant in human-altered habitats yet virtually absent from unmodified forest.

In the present chapter, we ask why exotic birds often proliferate in urbanized environments. This involves addressing (1) why they are able to succeed in such environments and (2) why they rarely expand to more natural habitats. While these two questions may be seen as the two sides of a same coin, each also has their own singularities. The concept of disturbance is central to resolve the first question. By altering natural environments, humans may be creating new niche opportunities for invaders and reducing biotic resistance, making the new environments more susceptible to be invaded (Case 1996). While this hypothesis alone could explain why exotic birds are common in urbanized environments, two alternative explanations

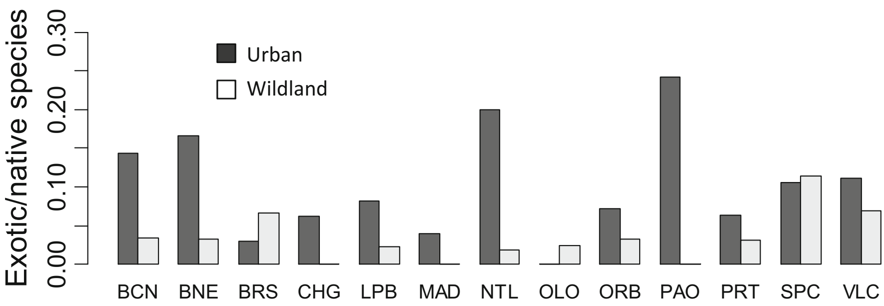

Fig. 5.1 Ratio of exotic-to-native avian species in urban habitats and non-urban surrounding wildland for several regions worldwide. Abbreviations correspond to BCN = Barcelona, BNE = Brisbane, BRS = Bristol, CHG = Cameron Highlands, LPB = La Paz, MAD = Madrid, NTL = Newcastle, OLO = Olongapo, ORB = Orebro, PAO = Palo Alto, PRT = Pretoria, SPC = La Palma, and VLC = Valencia. For references, see Sol et al. (2014)

also need to be considered. On one hand, although human-altered environments may seem highly susceptible to be invaded, this may simply reflect that many more species have been introduced there. On the other hand, an association of exotic birds with urbanized habitats is also expected if traits associated with invasion success and the ability to thrive in close proximity to humans are related (Ehrlich 1989). We argue that these two alternatives also contribute, along with disturbances, to explain the proliferation of exotic birds in human-altered environments.

In contrast, the question of why exotic birds rarely expand to more natural habitats is less clear, although some hypotheses have been advanced. Higher biotic resistance and stronger environmental filtering in more natural communities are obvious explanations (Diamond and Veitch 1981), yet a number of alternatives exist, including insufficient time for the invader to spread or behavioural preferences for human-altered habitats. We discuss these hypotheses and suggest that the study of the few exceptions of exotic birds invading natural environments provide unique opportunities to tease them apart.

5.2 Why Are Exotic Birds Able to Succeed in Human-Altered Environments?

5.2.1 Susceptibility of Urban Environments to Avian Invaders

Human-induced disturbances may facilitate invasions by increasing resource opportunities and reducing biotic resistance (Case 1996). A resource opportunity refers to the availability of resources on which an invader depends (Shea and Chesson 2002) and can arise from the non-random loss of native species in urbanized habitats (Simberloff 1995). This loss results from the drastic environmental alterations associated with urbanization, which includes a replacement of natural vegetation by built structures, a shift from natural to artificial resources and a higher frequency of human disturbances (Marzluff et al. 2001; McKinney 2002). These alterations may act as strong environmental filters by limiting the persistence of those species incapable of tolerating them (Evans et al. 2011; Sol et al. 2014).

Although a reduced species diversity may imply the absence of entire functional groups (Simberloff 1995), human activities offer at the same time a variety of novel resource opportunities to which native species have had little opportunity to adapt (MacLeod et al. 2009). These include food supplies like artificial feeders and garbage and nesting sites such as holes and cavities in buildings. If a species is able to exploit these opportunities while tolerating the human presence, this may facilitate population growth and establishment in the novel region (for a review of the influence of these factors on the establishment of native species in cities, see Tomiałojć 2016).

The combination of low diversity of native species and high levels of novel niche opportunities may make communities less resistant to invaders that are able to exploit these opportunities (Shea and Chesson 2002). First, the number of potential competitors should not only be reduced in urbanized environments but the few that thrive there may have had insufficient time to adapt to efficiently exploit the local resources. Second, the pressure from enemies should also be reduced due to the release from their natural predators and parasites, which usually are not introduced with the exotic species (Shochat et al. 2010). Finally, human-related alterations may generate spatial and temporal environmental heterogeneity through the fragmentation of natural habitats and the creation of artificial environments. A structurally heterogeneous region may provide a greater array of microenvironments, increasing the likelihood that the invader encounters a favourable niche not monopolized by native species.

Although still limited, evidence is accumulating that human-induced environmental alterations facilitate invasions by opening resource opportunities and decreasing biotic resistance from resident native species. For example, Barnagaud et al. (2013) reported that in New Zealand, exotic and native bird species segregate along gradients of anthropogenic disturbance, with exotic species being more common in disturbed environments. Interestingly, native and exotic species overlapped little in functional traits related to habitat selection. Hence, habitat segregation patterns are probably mediated more by environmental filtering processes than by competition at landscape and local scales.

Likewise, in SE Australia, the success of exotic birds in highly urbanized environments does not seem to be associated with their competitive superiority over native birds but with the existence of resource opportunities derived from human activities (Sol et al. 2012a). Thus, the most successful avian invaders were generally smaller and less aggressive than many natives and were excluded from experimental food patches where competition was strong. Instead, the most successful exotic birds were those less afraid of taking advantage of food opportunities provided by humans, consistent with the view that exotic species that opportunistically exploit the abundant food accidentally or deliberately produced by human activities may reach high population densities (Marzluff 2001; Shochat et al. 2010; Møller et al. 2012).

This is not to say that contest competition is irrelevant during the establishment stage. In ring-necked parakeets (*Psittacula krameri*) introduced to southern Spain, detailed observations by Hernández-Brito et al. (2014) suggest that these parakeets are outcompeting native species with similar nest-site requirements. However, there is currently little evidence that traits that provide competitive advantages favour establishment in birds (Duncan et al. 2003). In contrast, as discussed in later sections, evidence is accumulating for a set of traits that may facilitate the adoption of novel niches with no need of aggressive displacements.

5.2.2 Adaptations to Find a Niche in Urbanized Environments

While the physical environment may in some cases have a negligible impact on habitat invasibility (Von Holle and Simberloff 2005), the existence of environmental filtering suggests that most birds do not tolerate well the drastic alterations associated with urbanization (Sol et al. 2014). If so, why are many exotic species so successful in urbanized environments? Do they have adaptations that allow them to be successful urban dwellers? A number of features have been found to predict invasion success in birds, including behavioural plasticity (see Miranda 2016), ecological generalism and particular aspects of their life history (Sol et al. 2012b). Importantly, these same traits have also been associated with tolerance to urbanization (Table 5.1).

A major feature of successful avian invaders appears to be behavioural plasticity. Ever since Mayr (1965), behavioural plasticity has been considered a main feature of successful avian invaders on the grounds that a species that accommodates its behaviour to the demands of the new environment is generally more likely to succeed than a species that persists with the behaviours of its place of origin. Indeed, there is evidence showing that the likelihood of establishment in novel regions increases with the propensity to learn new behaviours and the underlying neural substrates (Sol et al. 2005, 2008; Amiel et al. 2011). Behavioural adjustments (Kark et al. 2007; Lowry et al. 2012; Sol et al. 2013), together with the associated brain structures (Maklakov et al. 2011, but see Sol et al. 2014), are also

Table 5.1 Evidence for common traits facilitating invasion success of exotic birds and tolerance of native birds to urbanization. Abbreviations: NS = non-significant; + = Supporting evidence

Traits and metrics	Evidence for urbanization	Sources	Evidence for invasions	Sources
Behavioural flexibility				
Relative brain size	NS, +, NS, +, NS	a–e	+, +, +, +	f–h, m
Innovation propensity	NS, +, +	a, i, j	+, +, +	f–h
Niche features				
Niche position	+, +	c, e		
Niche breadth	+, +	b, e	+, +, +	k, l, m
Life history				
Brood value	+	e	+	m
Human tolerance				
Mean flight initiation distance (FID)	+, NS, NS	n, b, i	None	o
FID intraspecific variation	+, +	b, p	+	q

References: a = Kark et al. (2007), b = Carrete and Tella (2011), c = Evans et al. (2011), d = Maklakov et al. (2011), e = Sol et al. (2014), f = Sol and Lefebvre (2000), g = Sol et al. (2002), h = Sol et al. (2005), i = Møller (2009), j = Sol et al. (2013), k = McLain et al. (1999), l = Cassey et al. (2004), m = Sol et al. (2012b), n = Møller (2008), o = Sol et al. (2012a), p = Møller (2010), q = Sol et al. (2011)

deemed essential to persist in urban environments. These include the need to develop innovative foraging techniques to exploit novel foods, to habituate to the human presence and to learn how to avoid risks like being run over by cars (Møller 2008, 2009; Liker and Bókony 2009; Sol et al. 2011, 2013; Husby and Husby 2014).

In addition to behavioural plasticity, a broad ecological niche should also increase the likelihood that an invader can find the necessary resources and suitable physical conditions in the novel environment (Ehrlich 1989; McLain et al. 1999; Cassey et al. 2004). In birds, species that are either dietary or habitat generalists are more likely to establish themselves successfully in new regions (McLain et al. 1999; Cassey et al. 2004). Ecological generalism can also increase urbanization tolerance, as evidenced by the fact that urban exploiters have broader environmental tolerances than avoiders, at least in terms of habitat breadth and geographic range size (Bonier et al. 2007; Evans et al. 2011; Sol et al. 2014).

Finally, recent evidence suggests that the life history of birds also affects their invasion success. Specifically, successful avian invaders appear to prioritize future over current reproduction, either by having a long reproductive life or by reproducing more frequently (Sol et al. 2012b). This strategy reduces the costs of a reproductive failure due to bad decisions (e.g. nesting in an inappropriate site) and allows skipping a reproduction when conditions are unfavourable. The possibility to delay reproduction increases the time available for acquiring environmental information and for improving performance in exploiting the resources and avoiding enemies. A life history strategy that prioritizes future returns also seems to characterize urban dwellers, according to a recent global comparative analysis (Sol et al. 2014). This is illustrated by dark-eyed juncos recently established in an urbanized environment in San Diego (California), which lay more clutches per season than those living in their traditional habitats and hence compensate for the lower success of each breeding attempt (Yeh and Price 2004).

5.2.3 Selective Filters Favouring Adaptations to Urbanized Environments

While there is increasing evidence that traits associated with urbanization also favour establishment in human-driven introductions, the question arises of why these features should be present in species selected for introduction. In fact, many introduced species are neither particularly ecologically and/or behaviourally plastic nor have a future returns life history strategy, which in part explains the high rate of failure in avian introductions (Duncan et al. 2003; Sol et al. 2012b). Still, the fact that a substantial fraction of introduced species do have adaptations to persist in urbanized environments warrants explanation. One possibility is that these properties are widespread among birds, so even if the species were selected at random, many should possess them. However, this is unlikely to be the case for all traits. Indeed, the combination of adaptations that make species successful urban dwellers does not seem to be very common in nature (Sol et al. 2014). Alternatively, the same process of transport and introduction may select for species with the adaptations needed to persist in urbanized environments. In fact, it has been known for some time that introduced birds are a distinctly non-random subset of the world's birds (Blackburn and Duncan 2001; Duncan et al. 2003). Because species with enhanced behavioural plasticity, broad ecological niches and life histories that prioritize future reproduction are more likely to be abundant close to human settlements (Evans et al. 2011; Sol et al. 2014), they should also be more readily available for introduction. Even species that thrive in urban environments thanks to more specialized adaptations can be favoured in introductions if they are more readily available.

Urban species may be easier to obtain not only because they live close to humans but also because they can attain higher densities in these environments due to the release from enemies and the high availability of resources (Shochat et al. 2006; Møller et al. 2012). Because they are easier to obtain, it is even possible that urban birds are introduced in higher numbers than non-urban birds. This is relevant because a large propagule size is known to facilitate establishment by reducing the risk of extinction by demographic stochasticity and Allee effects (Lockwood et al. 2005; Simberloff 2009) as well as by enhancing phenotypic variation (Holt et al. 2005). However, whether urban birds are more likely to be introduced in large numbers than non-urban birds remains to be tested.

Not only are some species more available for introduction than others because of their higher abundance close to human settlements but the subsequent stages in the invasion process can also filter species according to their features. This is because only those birds with appropriate phenotypes negotiate any given stage of the invasion process successfully (Chapple et al. 2012). Such a 'selective filter' may sometimes favour phenotypes better adapted to urbanization (Fig. 5.2). Møller et al. (2015), for example, proposed that the adaptations that enable birds to live in the proximity of humans, like reduced fear to humans, can also better predispose them for coping with capture, transport and introduction. Likewise, animals that are flexible in their behaviours and that have broader diets and environmental tolerances should better cope with captivity as they can adjust to such conditions more readily (Mason et al. 2013). While there is current controversy regarding whether there exist some traits that favour crossing all the stages of the invasion process (Chapple et al. 2012), the existence of traits associated with human-altered environments emerges as one of the few plausible generalizations.

The 'selective filter' can further strengthen the relationship of birds with humans if individuals are kept in captivity for several generations before being released, as this can artificially select for traits that facilitate living and reproducing close to humans (McDougall et al. 2006; Carrete and Tella 2008). Artificial selection for frequent reproduction in their domestic ancestors is thought to allow feral pigeons to increase offspring productivity (Janiga 1991), contributing to compensate for the high mortality rate associated with starvation and car accidents. Nevertheless, if an exotic species has been bred in captivity for long periods of time, artificial selection can have eroded many of its behaviours and other phenotypic traits needed to survive in nature (McDougall et al. 2006; Carrete and Tella 2008; Sol 2008). This

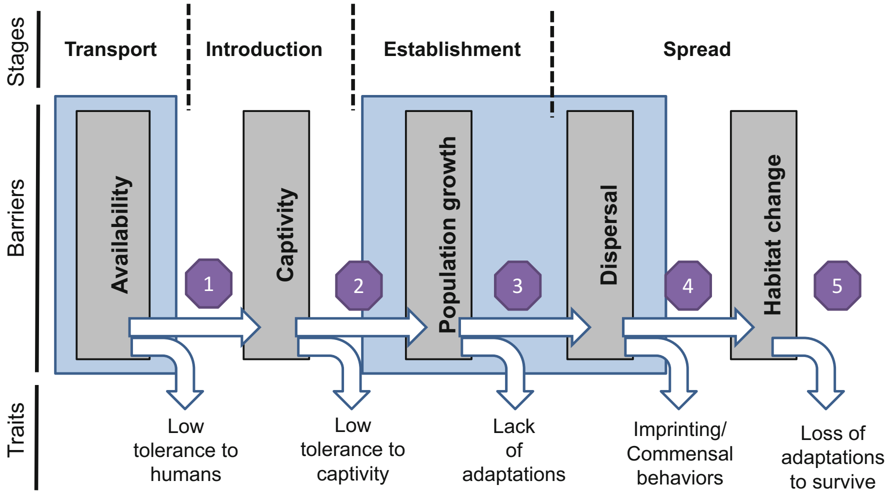

Fig. 5.2 Successful invasion of a new location involves a four-stage process (Blackburn et al. 2011). Each stage selects for different traits, both among and within species, which may in part explain why exotic birds mostly proliferate in urbanized environments. The species must firstly be deliberately or accidentally transported (transport stage) and introduced (introduction stage) to a new location outside their native range; this is more likely if the species exhibits tolerance to humans and human-altered environments (barriers 1 and 2), thereby increasing availability and enhancing survivorship in captivity. Next, the species must establish a self-sustaining population in the novel environment (establishment stage); this further sorts out birds according to traits that enhance the probability of finding an appropriate niche in human-altered environments, such as behavioural plasticity and broad ecological tolerances (barrier 3). Then, the population must subsequently increase in abundance and expand their geographic area (spread stage); spread towards more natural habitats can be limited by behavioural decisions that force individuals to settle in urbanized environments (barrier 4). Finally, the expansion to more natural environments may be further limited by a lack of appropriate adaptations (barrier 5)

is less of a problem in species that rely on resources directly provided by humans. The high invasion success of feral pigeons, for example, is in part related to the exploitation of the large amount of food provided by people (Sol 2008).

Humans could not only unintentionally select species for introduction that are capable of thriving in cities, but may also enhance their establishment success by yet another way, releasing them in urbanised environments. As humans are more likely to accidentally or deliberately introduce organisms close to where they live, this predicts a certain association between exotic species and urbanized environments. In Barcelona, for example, the earliest observations of the currently large population of monk parakeets (*Myiopsitta monachus*) were near the zoological garden, from where they presumably escaped (Batllori and Nos 1985). Likewise, for European settlers in the eighteenth and nineteenth centuries moving to the Americas, Australia, New Zealand and South Africa, introducing birds close to their homes was a common practice in their attempt to recreate their European homeland (Duncan et al. 2003). By accidentally transporting exotic birds from one city to another, humans may have also favoured their spread.

5.3 Why Are Exotic Species Unable to Expand to More Natural Habitats?

Although the reasons why exotic birds do not expand to more natural habitats are largely unknown, for birds limited dispersal capabilities does not seem to be the explanation considering their well-developed flying capabilities. Moreover, cities are often located within mosaics of natural habitats, again suggesting that distance is not limiting spread. Alternative explanations are thus needed.

Following our previous arguments, an obvious explanation for the failure of exotic birds to expand to more natural surrounding habitats is that they cannot persist there. This can occur because of higher biotic resistance of these environments, which is expected if these communities are more diverse and mature. Alternatively, the invader may lack adaptations to persist in such environments (Shochat and Ovadia 2011).

Other explanations need to be considered as well. First, many introduced populations might have had insufficient time to increase in numbers so as to generate enough propagules to expand to new habitats. Time lags between establishment and spread are commonly reported in the literature (Williamson 1996) and have been attributed to factors such as the time required to adapt to the new environment or changes in the way the invader interacts with native species (see Chapple et al. 2012; Hufbauer and Facon 2012). If time lags are the cause of some exotics being restricted to urbanized environments, we expect that the species expand the range of habitats used over time following classical habitat selection models that predict shifts to alternative habitats when the preferred ones become saturated (Křivan et al. 2008). There is indeed some evidence that avian invaders behave as habitat specialists during the earlier stages of the invasion process and subsequently relax their preferences when the preferred habitats become saturated (Sol et al. 1997; Kövér et al. 2015). However, there are also well-documented cases where an exotic bird has remained restricted to human-altered environments despite having had good opportunities to spread to surrounding natural habitats. In the city of Valencia, for example, 35 years after initial settlement of different Psittacidae species, they are still largely confined to the urban area (Murgui 2001; Murgui and Valentín 2003).

Second, exotic species can exhibit a strong preference for urbanized habitats in the new region. The singularity of urbanized environments may for instance favour strong habitat imprinting, making individuals to prefer settling in the habitat type in which they were born (Evans et al. 2009). If this mechanism is important, we would only expect shifts to more natural environments when urbanized environments become saturated and when the bird has enough plasticity to overcome the influence of imprinting. Alternatively, if species have been selected for traits that force them to live in close association with humans during the capture and transport, this can also enhance their preference to settle in urbanized environments once released. This can be particularly important when artificial selection has eroded the behaviours and other phenotypic features needed to survive in nature (McDougall et al. 2006; Carrete and Tella 2008), which may make the population highly dependent on human assistance. Feral pigeons (*Columba livia*), for example, still preserve some characters engendered through artificial selection during their ancestral period of domesticity, notably a disproportionally longer tarsus; this leg morphology appears to limit the use of food resources other than those directly provided by humans and, as a result, increases mortality when individuals have to search for their own food (Sol 2008).

While many exotic species are restricted to human-altered environments, a few have been able to invade more natural habitats. This is the case of the red-billed leiothrix, *Leiothrix lutea*, which has been able to establish itself in forests from the Western Mediterranean region and Japan. Combining historical information, phylogenetic analyses and field observations and experiments, Vall-llosera et al. (2016) reported that leiothrixes established themselves with relatively little resistance or significant consequences for most native species, reflecting the opportunist-generalist nature of both the invader and the invaded native community. Moreover, some of their key niche requirements were poorly represented in the native community, suggesting that the species is using an infra-utilized niche. While this fits well with the view that the existence of niche opportunities and reduced biotic resistance is crucial for the success of exotic birds, additional studies in other species invading natural habitats are warranted.

5.4 Conclusions

Human-altered environments may be particularly susceptible to invaders, but this alone is insufficient to understand the success of exotic birds in urbanized environments. We argue that if we want to further understand this, we need to see the invasion process as a chain of stages with different probabilities of being transited (Fig. 5.3). The adoption of such a framework highlights that the odds are high that an exotic bird ends up associated with urbanized environments if the species (1) is abundant in urbanized environments and hence more available for introduction; (2) has a higher chance to be successfully transported, as it is already habituated to humans; and (3) has a higher probability to be introduced in an urbanized environment, where most humans live. Given that habitats are altered by humans in similar ways worldwide, birds that do well in human-altered habitats in their native range should also perform well when introduced within similarly human-altered habitats (Ehrlich 1989; Hufbauer and Facon 2012). The existence of such human-mediated environmental matching is supported by two comparative analyses. The first study reported that species that use urban environments in their native regions are more likely to be successfully introduced outside their native ranges (Sol et al. 2002), although subsequent studies with broader samples failed to provide similar evidence (e.g. Sol et al. 2012b). More recently, Møller et al. (2015) tested the hypothesis with a stronger measure of urbanization tolerance based on changes in abundance between urban and rural habitats. They found that the most tolerant species were also more likely to succeed when introduced to Pacific Islands. While

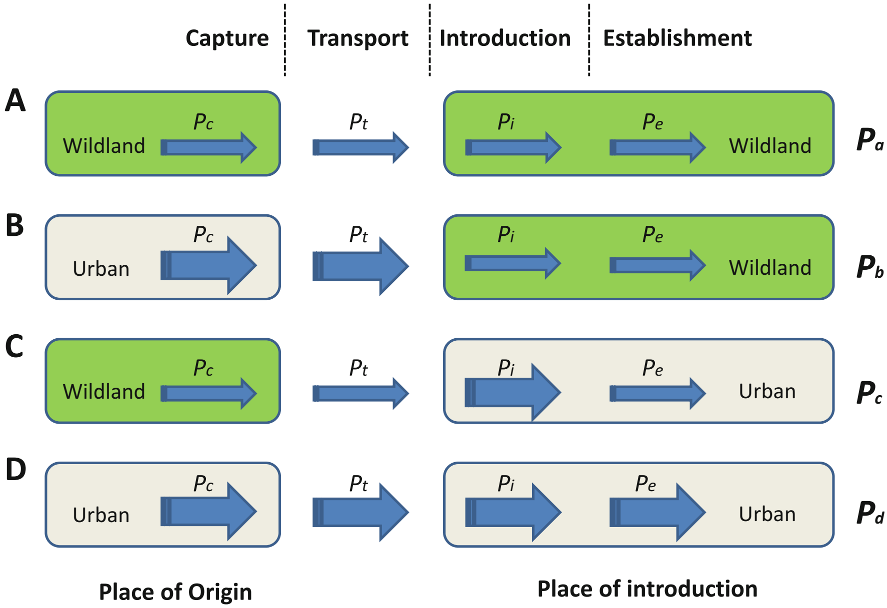

Fig. 5.3 Framework to understand why we expect many exotic species to be successful in urbanized environments. The scheme represents four scenarios defined by the habitats of origin and introduction of the exotic species (from A to D). The size of each arrow represents the probability that a species is captured (P_c), transported (P_t), introduced (P_i) and successfully established (P_e). These probabilities multiply along the pathway to determine the probability of observing an exotic species in the final habitat (P_a to P_d), with $P_a < P_b < P_c < P_d$

this result yields important support for the existence of human-mediated environmental matching, more studies are needed to further support the pattern and unravel the underlying mechanisms.

Understanding why exotic birds are mostly restricted to human-altered environments allows resolving a major paradox in invasions biology, namely, why exotic species that have had little opportunity to adapt to the novel environment are able to proliferate there and even become more abundant than many native species (Simberloff 1995; Case 1996; Sax and Brown 2000). According to the framework we propose in this chapter, the success of many avian invasions is not a paradox. Rather, it may be understood if we consider that (1) successful invaders are occupying infra-utilized or novel ecological niches associated with human activities that most native species are unable to use (Sax and Brown 2000; Sol et al. 2012a), and (2) exotic species possess the necessary adaptations to invade these niches because human activities facilitate environmental matching by determining which, where and how the species are introduced. Although our focus here is on birds, we suspect our conclusions must also apply to other organisms (see Bartomeus et al. 2011 for an example in plants).

5.5 Conservation Implications

The above conclusions have two main implications for conservation. The first is related to biotic homogenization, that is, the increased resemblance of biotas across different regions due to the extinction of native species and the introduction of exotic species. As pointed out by McKinney (2006), urbanization increases biological homogenization because the few species capable to persist in such environments become increasingly widespread and locally abundant across cities. Successful avian invaders that proliferate in urbanized environments not only contribute to the homogenization process in such environments but also scale up the effect to a global level (but see Aronson et al. 2014). This goes against the increasingly perceived role of cities as future reservoirs of biodiversity (Secretariat of the Convention on Biological Diversity 2012).

The second implication for conservation concerns the impact of invaders. If exotic birds are restricted to use altered environments, it follows that their impact over native species should be more reduced. This fits well with evidence that exotic birds have caused few extinctions in the past (Sax and Gaines 2008). Although Case (1996) reported a positive relationship between the numbers of established and recently extinct bird species at locations around the world, this relationship does not arise because introduced birds cause the extinction of native species as most extinctions occurred prior to bird introductions. Rather, this pattern may reflect that human disturbances simultaneously reduce the diversity of native species and create new habitats favourable for the establishment of introduced birds (Case 1996; Duncan et al. 2003). Sax and collaborators (2008) even suggested that established exotic birds could contribute to increase biodiversity at local and regional scales. However, the fact that most exotic birds occur in disturbed environments indicate that they do not simply compensate the loss of native species but that they often play different functional roles in the ecosystem.

In any case, the conclusion that exotic birds do not generally pose risks for native species should be taken with caution. Extinctions can take time, and hence it is possible that some avian introductions are too recent for the impact to be observed. Moreover, the possibility remains that some exotic birds have not yet had time to expand to more natural habitats. Although some of the reasons that link exotic species to urban environments may also explain their limited success in more natural environments, the reasons why they rarely expand to more natural habitats are largely unknown. Given the difficulties to investigate why a species is absent from a particular habitat, the alternative to shift the focus to those few exotic birds that are present in natural habitats is likely to represent an important avenue for future research.

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