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COMMENT

How useful are urban island ecosystems for defining invader patterns?

Biological invasions are pervasive, alter ecosystem sustainability, and can reduce native biological diversity (Vitousek *et al*. 1996). Ecologists are scrambling to predict where and when new invaders may strike (Lodge 1993; Fagan *et al*. 2002). Urbanization has created a number of new ecological niches which, after remaining empty for some time, are increasingly being colonized or invaded by vertebrates (Erz 1966). One of the major disputes in evolutionary biology concerns the rate at which species evolve to occupy new niches (Diamond 1986). How quickly are animals adapting to these new habitats and what makes them successful colonists?

The island character of urban areas also makes them suitable for testing hypotheses related to invasion biology. Animal or plant populations may be isolated in towns (Cihakova & Frynta 1996) supporting the idea that colonization or invasion processes could be studied in towns in similar ways to those used on oceanic islands (Davis & Glick 1978). Although McDonnell and Picket (1990) have clearly underlined their advantages to ecology, urban ecosystems have not interested many researchers.

Urban areas can be used to define characteristics of invader species. We define invaders in urban contexts and explain why urban areas are a good system to identify traits of invader species. We also propose ideas for further research. This is restricted to terrestrial habitats because aquatic habitats are scare in urban environments and plants species have the capacity to remain in the soil as seeds even after drastic modifications of the area. These studies are therefore applicable for terrestrial animals.

Predicting invaders

Williamson (1996) and Shigesada and Kawasaki (1997) defined a species as 'invader' when it establishes itself in a new geographical area (out of its normal biogeographical range) with or without human intervention. We expand this view by considering that invasion also occurs when a species establishes itself in a new habitat even within its geographical range. For example, the herring gull *Larus argentatus* is a recent invader in French urban areas. This wider definition need not encompass the environmental damage sometimes linked to 'invader species'.

Predicting species that are likely to be successful invaders has been an important goal of biodiversity conservation. Three intertwined factors can be considered for prediction (Labisky *et al*. 2003): (1) species-level factors such as reproductive (Pysek 1998), morphological (McLain *et al*. 1999) or behavioural (Sol *et al*. 2002) patterns, including competitive capacity and range of environmental tolerance (Ehrlich 1989); (2) environment-level factors, such as niche opportunities and ecosystem nature (Levine 2000; Shea & Chesson 2002); and (3) human-level factors, such as landscape modifications or introduction patterns (number of releases, number of individuals released; Green 1997).

Although communities with high species richness seem more resistant to invasion (Elton 1958), the biotic and abiotic quality of receiver environments remains quite difficult to define. Focusing on measurable traits that make species good invaders might be easier. Although Crawley (1987) has stated that it is also difficult to predict invaders from the species characteristics, others have pointed out that life-history traits might be useful tools to predict invader species (Riccardi & Rasmussen 1998; Kolar & Lodge 2001).

In our view, definition of invader characteristics is a poorly used challenge for predictive ecology. The majority of the earlier studies defining invader characteristics were conducted on oceanic islands and involved introduced species. By examining invaders' characteristics in other environments, like urban habitats, we could increase the predictability of some traits, especially if

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we are interested in spontaneous invasion. Urban areas are good experimental landscapes to study the typology of characteristics of invaders.

Why urban environments provide a good model ecosystem to identify characters of invaders

Urban areas appear to be a good model system to study biological invasion, excepting fresh waters, because isolated habitats are rare in terrestrial landscapes. One of the most cited factors in invasion biology is the introduction mechanism, which relates to transportation, facilitation by humans and the number of releases (Green 1997). Some successful urban species, like the house sparrow *Passer domesticus* and brown rat *Rattus norvegicus*, have expanded their ranges with the direct help of humans. However, for most species colonizing urban environments, intrinsic biological factors are more important than external factors. Furthermore, the urban matrix acts as a filter for the movement of many species, but is not a total barrier for invading species. Therefore, to colonize cities, species do not necessarily need help from people; it is enough if the species characteristics are suitable for urban life. Thus, it is easier to separate biological characters from introduction factors in towns than it is in other environments.

Urban ecosystems have many characteristics that attract invading species. For example, urban environments have fewer predator species (Tomialojc & Profus 1977; Sorace 2002) and low community diversity (Clergeau *et al.* 1998; Jokimäki & Huhta 2000). In cities, there is a large number of habitats in which resources are not limiting or in which the low population density means that there is no heavy competition for limited resources. In addition, repeated disturbances in urban environments might decrease the competition between species. In urban environments, new gaps are being created and there will always be competition-free situations that allow new species to invade them. Based on the concept of 'niche opportunity', that areas with low species richness have a low invasion resistance (Shea & Chesson 2002), urban ecosystems have low invasion resistance.

Tolerance of new habitat and new interspecific contexts is more highly expressed in the colonization/invasion of urban systems than in any other patch system. Gaston and Lawton (1990) suspected that the most abundant and widely distributed species are also dominant in most environments within their native range. These species can also become established as colonists more easily because they are capable of tolerating (and evolving within) a wide range of abiotic conditions. We agree with Sax and Brown (2000) that the habitat and resource tolerance of a species could be a key for colonization and dominance in new environments. Urban island ecosystems offer an opportunity to identify these tolerance patterns and to determine a general biological profile of the most probable spontaneous colonizers/invaders.

It is also important to note that urban environments potentially enable us to obtain adequate numbers of samples for statistical analyses. In general, lists of urban species are quite similar in towns throughout the world, and shared species patterns in towns are regularly reported by authors independently of geographical location (Clergeau *et al.* 1998). This indicates that urbanization favours particular traits of species, for example plastic habitat and food requirements (Jokimäki & Suhonen 1993; Clergeau *et al.* 1998), or small body size (Sustek 1987). As general characteristics of towns are similar throughout the world, we could better control the possible effects of habitat quality on the probability of invasion in towns than in other environment types.

Suggestions for further research

We have restricted our view to the final stage of the colonization/invasion process (permanent establishment of species) but, in the future, we must consider each step of the invasion process (arrival and establishment, spread). By doing so, a more accurate definition of invaders could be formulated (Heger & Trepl 2003).

The expression of an invasion mechanism and a tolerance capacity is more complex in suburban areas than in urban cores. In order to control environmental conditions and arrival frequencies, we have to concentrate our research on the core of urban systems; in other words on the oldest parts of towns that are normally most isolated from the surrounding matrix.

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A multinational research programme where occurrences (or more ideally abundance data) of species are collected using the same study design and common survey method from both the urban core and surrounding matrix of the town could produce lists of species that are, or are not, able to colonize cities. From these lists of species, we could measure ecological, morphological and behavioural characteristics of invader species and correspondingly define the general profile of successful colonizers/invaders. This methodology could be applied to different groups of animals in which there are sufficient numbers of species, such as birds and insects. By comparing the results for different taxa, we could understand in more detail the characteristics that make some species more successful invaders than others.

In conclusion, the study of colonization/invasion in urban systems should increase our knowledge of the 'ideal invader' and reveal new patterns and processes related to invasion biology. Urban environments might provide a new template for biological invasion research. We urgently need arguments to remove some potential invaders from the trade in exotic species (Jenkins 1996), and to foster more rapid decision-making in the management of some invader species that can become pests (Clergeau & Mandon-Dalger 2001; Clergeau *et al*. 2004).

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