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8 **Island biogeography of insect conservation in urban green spaces**

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SUMMARY

Because of their isolation, biotic communities of urban green spaces are expected to be similar to those of oceanic islands. This should be particularly true for insects, which represent an important component of urban faunas. The equilibrium theory of island biogeography (ETIB) allows the formulation of some hypotheses about the influence of geographical characteristics of green spaces on insect species richness and extinction risk. Based on island biogeography principles, we present eight predictions about how green space characteristics should influence insect species richness and loss. We analysed current literature to see which predictions were supported, and which not. We found that many studies gave outcomes that support ETIB predictions, but effects including of species ecology, matrix characteristics and geographical location of the city varied considerably; we found no support for some of these predictions in the literature that we reviewed. Most of the available studies dealt with patterns in species richness, whereas insect species loss has been rarely investigated. Future developments in the application of island biogeography principles to urban insect conservation should address temporal trends in species persistence and the analysis of species co-occurrence and nestedness.

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INTRODUCTION

More than half the world's human population lives in cities and this proportion is projected to grow in the next years (United Nations 2014). Urbanization is therefore considered one of the most important threats to biological conservation worldwide (McDonald *et al.* 2013). On the other hand, the urban green infrastructure may host a high variety of biotopes and species, sometimes greater than those of the surrounding rural areas (Angold *et al.* 2006; Jones & Leather 2012). Thus, urban green spaces may represent important biodiversity reservoirs and there is increasing interest in their inclusion in urban planning and global biodiversity conservation actions (Secretariat of the Convention on Biological Diversity 2012). Because urban green spaces are generally small, they may be of less value for large animals, but can be important for organisms that can survive in small areas or that form metapopulations, such as small sized mammals, reptiles and most invertebrates (Angold *et al.* 2006; Hunter & Hunter 2008; Fattorini 2011a, 2011b; Jones & Leather 2012).

From the perspective of the organisms that live in urban green spaces, the urban environment can look like a set of habitat islands (the green patches where they live) separated by more or less inhospitable environments (the matrix represented by the built up areas). Thus, biotic communities of urban green spaces are expected to have population dynamics similar to those of islands.

Important insights on the interplay of processes and patterns in evolution, ecology and biogeography have come from insular studies (Lomolino *et al.* 2010). In particular, the equilibrium theory of island biogeography (ETIB) proposed by MacArthur and Wilson (1963, 1967) to explain variations in species number on islands turned into one of the most productive research programmes in ecology (Lomolino *et al.* 2010). According to the ETIB, species richness on islands is the result of immigration/colonization and extinction processes, in turn regulated by physical features of the islands, such as area and isolation (Lomolino *et al.* 2010).

Providing a simple mechanistic model of variation in species richness based on extinction and colonization rates, the ETIB had impact far beyond its original scope and influenced basic biogeographical thinking. If urban green spaces are islands in a 'sea of concrete', the principles of the ETIB should also apply to the urban environment.

The ETIB has in fact inspired biodiversity research in urban areas since the inception of urban ecology (Faeth & Kane 1978) and research in urban habitats has been frequently addressed to investigate how species richness is influenced by characteristics of green spaces (e.g., Clarke *et al.* 2008; Sattler *et al.* 2011; McDonnell & Hahs 2013). From a more formal point of view, several ETIB predictions can be applied to the urban green spaces as islands (Fattorini 2016). These ETIB predictions are reformulated here and involve the influence of green space characteristics on patterns of species richness (Predictions 1-4) and processes of extinction/colonization (Predictions

77   5-8) (Fig. 1).

78   **Prediction 1**: Species richness should increase with island area (the so-called species-area

79   relationship, SAR) because larger islands will tend (1) to support larger populations, (2) to have

80   higher habitat diversity or heterogeneity (the so-called 'habitat diversity hypothesis') and/or (3) to

81   be larger targets for potential colonists (the so-called 'passive sampling hypothesis'). Distinguishing

82   between these alternative explanations for the SAR is usually difficult (see Fattorini *et al.* 2015).

83   However, at least under certain circumstances, it is possible to statistically separate the contribution

84   of area *per se* from that of habitat diversity. Habitat diversity is an elusive concept and may largely

85   depend on the concerned group. In the few cases that considered habitat diversity for insects of

86   urban green spaces, it was expressed as the number of vegetation types (Clarke *et al.* 2008), the

87   Shannon index of land use types (Matteson & Langellotto 2010), biotopes (Shwartz *et al.* 2013) or

88   plant diversity (Fortel *et al.* 2014). The effect of area *per se* may be due to both the passive

89   sampling hypothesis and the persistence of larger populations. These two explanations might be

90   distinguished by using data on species abundance and immigration rates.

91   **Prediction 2**: A typical assumption of reserve design is that a circular shape is better than an

92   elongated or indented one because a more rounded shape should reduce edge effects, and hence

93   should allow the persistence of a larger number of interior species (Yamaura *et al.* 2008; Kotze *et*

94   *al.* 2012; Soga *et al.* 2013). This assumption is not strictly derived from the ETIB, but it is usually

95   reported as one of the implications (e.g. Triantis & Bhagwat 2011). Because not all the area of a

96   green space can be suitable for insects, it is that of the native habitats within there that may be

97   important for insect conservation. Thus, species richness is expected to increase with circularization

98   of fragments of native habitats within green spaces, if not with the shape of the entire green space

99   (Sisk *et al.* 1997; Davies *et al.* 2001; Yamaura *et al.* 2008).

100   **Prediction 3**: Species richness should be inversely correlated with the green space distance

101   from source areas. In the ETIB framework, source areas may be either the mainland or other, nearby

102   islands. In the case of urban green spaces, the mainland is represented by the rural areas

103   surrounding the cities, whereas other green spaces may act as nearby islands. In most organisms,

104   including many insects, species richness tends to decline from the periphery (where more natural

105   habitats occur) to the most densely built-up areas of the urban core (the so-called urban-rural

106   gradient, Adler & Tanner 2013; New 2015). With reference to the ETIB, the landscapes at the

107   periphery of a city should act as a 'mainland', and hence species richness should decrease from

108   peripheral to city centre green spaces (McIntyre 2000). Since less isolated sites are expected to be

109   more easily colonized, i.e. to receive more immigrants, species richness in an urban green space

110   should also increase with its proximity (or connection) to other green spaces that can act as a

111   mainland or a stepping stone island (Magura *et al.* 2001).

112   **Prediction 4**: Species richness should increase with the extent of native habitats within each

113   green space. Species richness of insects that are strictly associated with humans (e.g., parasites) may

114   increase with urbanization. However, most insect species tend to decline with the reduction of

115   native habitats (New 2015). Therefore, fragments that include remnants of native habitats should

116   host more native species that depend on these habitats and, hence, more species in general

117   (Donnelly & Marzluff 2004).

118   **Prediction 5**: Under ETIB assumptions, species richness in urban green spaces should result

119   from a balance between local extinctions and continuous immigration. If the cities were in a steady-

120   state, immigration and extinction would be in equilibrium. However, because urbanization tends to

121   make green spaces progressively smaller, more isolated and less hospitable, species immigration is

122   probably insufficient to compensate for species loss (see Fattorini 2011b, 2013). Thus, although

123   most urban green spaces benefit from continuous immigration, their increasing isolation

124   progressively reduces the immigration rate of most species. The species that occur in urban green

125   spaces are nested subsets of the fauna inhabiting the rural areas surrounding the city. Of course,

126   immigration processes may lead a green space to gain a new species from the rural areas (i.e. the

127   mainland), but because extinction rates likely exceed new arrivals of individuals belonging to new

128   species or to species already occurring in a given green space, an increasing excess of extinction is

129   expected over long periods. Under this assumption, extinction levels should be correlated negatively

130   with green space size, because larger areas support larger populations that are less vulnerable to

131   demographic oscillations, genetic drift, inbreeding, and reduced heterozygosity (Lomolino *et al.*

132   2010).

133   **Prediction 6**: Extinction levels should correlate negatively with circularisation of the green

134   spaces or of their native habitats because more rounded shapes should reduce the negative impact of

135   edge effects (Davies *et al.* 2001). Also, more circular shapes should promote conspecific

136   interactions and positively affect dispersal rates (Diamond 1975). By contrast, elongated shapes are

137   expected to intercept less immigrants, and hence colonization rates should decline with decreasing

138   circularization.

139   **Prediction 7**: Extinction levels should be negatively correlated with proximity to areas that

140   can serve as sources of immigrants, such as other green spaces and rural areas. This prediction

141   follows from the basic assumptions that: (1) where there is more urban green space, there is more

142   likely to be enough suitable environment to sustain a metapopulation (Davis 1979); (2) higher

143   connectivity reduces the effects of genetic isolation (Davis *et al.* 2001) and facilitates immigration;

144   (3) small green spaces, even if unable to sustain a stable population of a given species, may sustain

145   individuals that are dispersing towards more suitable areas (Thomas *et al.* 2000); and (4) extinction

146   is negatively correlated with distance from the city centre because the multiple negative effects of

147 urbanization tend to diminish from the city centre to the most peripheral sectors (McKinney 2008)

148 and more peripheral green spaces are closer to the areas that are sources of immigrants (Dias 1996)

149 and can benefit from rescue effects (Gosselin 1996) and increased colonization rates.

150   **Prediction 8**: Extinction levels should be negatively correlated with the extent of native

151 habitats, because larger habitats increase the long-term viability of populations (Andrén 1994;

152 Fahrig 1997; Donnelly & Marzluff 2004).

153   These predictions can be retrospectively used to investigate if the ETIB can be applied to

154 urban insects. Despite the importance of island biogeography in urban ecology, there is no review of

155 how the principles of ETIB can be applied to the urban environment. The aim of the present paper

156 is to establish if these predictions are confirmed by the current literature on urban insects. This is

157 important not only in the context of urban ecology and conservation, but also from a general

158 biogeographical perspective. Urban green spaces are much easier to reach and to sample than

159 oceanic islands, thus providing intriguing opportunities to test and develop island biogeography

160 models. Thus, our review can also stimulate biogeographers to use urban green spaces as a test-bed

161 for their research.

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164 **METHODS**

165 The literature was searched using the Web of Science (WOS) databases from Thomson Reuters

166 (ISI) at first using the following retrieve terms: 'island biogeography urban' or 'island

167 biogeography city' or 'island biogeography cities'. A second search used keywords commonly used

168 to refer to insects in urban green spaces. To guarantee an extensive coverage, keywords were used

169 that resulted in relatively low search specificity, as recommended by Pullin and Stewart (2006).

170 Thus, the search was conducted by using the following combination of keywords: 'urban park*' or

171 'city park*' or 'green space*' or 'green area*' and 'insect*' (* indicating any ending possible). Our

172 searches were performed up to 1 October 2016, including no filtering related to the year of

173 publication type or language. Titles and abstracts identified by the searches were scrutinized and

174 relevant publications were manually selected. We searched for references reported in the retrieved

175 documents to avoid excluding important information not considered in WOS. In addition, all

176 papers, book chapters and books that might include references to the application of ETIB principles

177 to urban insects were searched. In particular, the references in two recent reviews of urban insects

178 (Jones & Leather 2012; New 2015) were searched. The presence of recurrent patterns, detection of

179 which is not strongly influenced by small methodological differences that can be found among

180 different papers were concentrated on. However, because methods varied among studies, the final

181 results presented in each paper more than the specific statistical tests that had been applied in each

182 case study, were considered.

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185 **RESULTS**

186 We retrieved 69 records with the terms 'island biogeography urban' and 25 with 'island

187 biogeography city' (or cities) for a total of 77 papers using the WOS. However, most of these papers

188 did not concern urban green spaces and only nine papers were potentially relevant. For example,

189 Baz & Monserrat (1999) dealt with apartments, Hamerlik & Brodersen (2010) with fountains, and

190 Clark *et al.* (2011) with true islands. The relative small number of papers retrieved by the WOS

191 indicated that few authors of urban ecological research had placed their results in a biogeographical

192 context, even if dealing with issues typical of island biogeography. The second WOS search

193 retrieved 70 publications, 14 of which were relevant to the present analysis, despite the authors not

194 placing their results in a biogeographical context.

195   The number of case studies dealing with each prediction varied considerably (Fig. 2, Table 1).

196 There were 31 case studies that could be attached to Prediction 1, which was therefore the most

197 frequently investigated. Predictions 2-4 were investigated in 10 or fewer studies. Predictions 5-8

198 were explicitly dealt with in only one study (see below).

199   The most frequently observed pattern consistent with ETIB predictions is an increase in

200 species richness (or other measures of diversity) with the area of green spaces (Prediction 1).

201 Studies reporting this positive relationship include species richness of various insect orders

202 (Coleoptera, Diptera, Homoptera, Hemiptera and Hymenoptera) in green spaces in California

203 (Bolger *et al.* 2000), Shannon–Wiener diversity of butterflies on roadside verges in south east

204 Finland (Saarinen *et al.* 2005), species richness of Diptera and Coleoptera in city parks in

205 Cincinnati (Faeth & Kane 1978), number of colonies of social wasps in urban gardens in Brazil

206 (Alvarenga *et al*. 2010), carabid species richness in urban green spaces in Bracknell (Leather &

207 Helden 2005), carabid species richness in road-enclosed forest patches in Helsinki (Koivula &

208 Vermeulen 2005), ant species richness in the Brazilian Cerrado (Pacheco & Vasconcelos 2007) and

209 in Tokyo and Chiba City (Yamaguchi 2004), bee species richness in New York (Matteson &

210 Langellotto 2010), butterfly species richness of green spaces in Halle and Saalkreis (Knap *et al.*

211 2008; Bräuniger *et al*. 2010) and Hokkaido (Yamaura *et al*. 2008), butterfly and pollinator species

212 richness in Paris (Shwartz *et al*. 2013), insect herbivores in abandoned city lots in Buffalo (Bod &

213 Maciejewski 2014) and tenebrionid species richness of green spaces in Rome (Fattorini 2014a). In

214 this latter study in Rome larger urban green spaces also had lower extinction rates, thus supporting

215 Prediction 5 (Fattorini 2014a). In general, area was identified as an important factor influencing not

216 only insect diversity, but also community composition (Davies & Margules 1998, Gibb & Hochuli

2002, Sadler *et al.* 2006, Fujita *et al.* 2008). However, no area effect was found for carabids (Weller & Ganzhorn 2004; Knap *et al.* 2008; Gaublomme *et al.* 2008; Bräuniger *et al*. 2010), bees (McFrederick & LeBuhn 2006), ants (Clarke *et al.* 2008), or butterflies (Bolger *et al.* 2000; Koh & Sodhi 2004; Öckinger *et al.* 2009; Matteson & Langellotto 2010; Lizée *et al.* 2012). Smith *et al.* (2006) also found no area effect for ants of London's green spaces, but they used species density as a measure of diversity, not richness. Similarly, Su *et al.* (2015) found a negative effect of green space area on overall insect density. This unexpected pattern can be explained by assuming that insect individuals disperse more widely in larger urban green patches, causing a decrease in individual number per unit area (Su *et al.* 2015). Excluding studies dealing with density, out of a total of 31 case studies considered in our analysis, 21 (68%) provided support for Prediction 1, and 10 (32%) did not.

Although area is considered a strong predictor of species richness, its effect may be a consequence of the fact that larger areas have a greater habitat heterogeneity (see Fattorini *et al.* 2015). For example, butterfly species richness in New York increases with park area and herbaceous plant species richness, suggesting that larger parks host more butterflies because their vegetation provides them with more food, greater habitat cover, and potential niches (Giuliano *et al.* 2004). However, neither area nor habitat diversity explained species richness of bumble bees and butterflies, respectively (Clarke *et al.* 2008; Matteson and Langellotto 2010). Similarly, plant diversity was not a predictor of wild bee species richness in green spaces of Lyon (Fortel *et al.* 2014) and habitat diversity was not important for butterflies and pollinators in Paris green spaces (Shwartz *et al.* 2013).

As regards the influence of habitat quality and extent, studies conducted in Central and Northern Europe and in North America, where cities grew into agricultural and forested landscapes, highlighted the importance of forest habitats (Schiller & Horn 1997; Clarke *et al.* 2008; Bräuniger *et al*. 2010; Heneghan *et al.* 2012; Kotze *et al.* 2012; Breuste *et al.* 2013). By contrast, for tenebrionids in urban Rome the percentage of forested area had a negative effect on species richness and species persistence (which contrasts with Predictions 4 and 8) (Fattorini 2014a). This is attributable to the low number of truly forest interior species among tenebrionids, which may also explain the lack of green space shape effects on species richness and extinction (in contrast with Prediction 2) , as well as the lack of forest shape effects on species extinction (in contrast with Prediction 6). Similarly, in Halle and Saalkreis (Bräuniger *et al*. 2010), there was a negative relationship between carabid richness and forests, probably because most of urban carabids are associated with open habitats. Other studies that failed to find a positive relationship between extent of pristine habitats and species richness included those of Pacheco and Vasconcelos (2007), Öckinger *et al.* (2009) and Koh and Sodhi (2004). Thus, out of 12 studies that dealt with it, seven

(58%) showed the importance of the extent of pristine habitats (typically forests), thus supporting Prediction 4, but five (42%) did not. The importance of a circular shape was detected for overall insect density (Su *et al.* 2015) and butterfly richness (Bräuniger *et al.* 2010). Also, Soga *et al.* (2013) found a negative effect of edge extent on forest carabids thus supporting the importance of a circular shape. However a negative effect of circularization was found for open-land butterflies of Hokkaido (Yamaura *et al.* 2008) and tenebrionids of Rome (Fattorini 2014b), which is opposite to Prediction 2. No effect of green space shape was found for butterflies (Koh & Sodhi 2004; Öckinger & Smith 2009), bumble bees (McFrederick & LeBuhn 2006), and ants (Clarke *et al.* 2008). Thus, out of nine studies that dealt with green space shape, only three (33%) supported Prediction 2.

Examples of isolation/connectivity effects on insect diversity (Predictions 3) include: (1) the positive influence of the proportion of surrounding land occupied by green spaces within 1 km of study sites for arthropod species richness in London urban gardens (Davis 1979) and butterfly species richness in green spaces of Malmö (Öckinger *et al.* 2009); (2) the negative influence of distance from natural areas (butterflies in Marseille; Lizée *et al.* 2012); (3) the positive effect of increasing distance from the city centre (ant density in Brazilian Cerrado; Pacheco & Vasconcelos 2007); (4) the total area of forests (i.e., reserves and fragments) within 2 km (butterflies of Singapore's green spaces; Koh & Sodhi 2004); (5) the negative influence of increasing urban cover for butterfly richness in South West Manchester and Mersey Valley, Manchester (Hardy & Dennis 1999); (6) the negative impacts of the extent of surrounding buildings and roads, traffic density and distance to suitable environments for carabid richness in Hamburg (Weller & Ganzhorn 2004). Distance between green spaces did not affect carabid and butterfly species richness in Halle and Saalkreis (Bräuniger *et al.* 2010) and distance from the city border was not correlated with butterfly species richness in Malmö (Öckinger *et al.* 2009). Green space connectivity in Rome did not enhance tenebrionid richness, probably because these insects form relict communities of species with low dispersal ability and hence with few chances to move from patch to patch (Fattorini 2014b).

Insect density in Beijin's green spaces was positively influenced by percentage of vegetated land and negatively by impervious surface (Su *et al.* 2015). However, connectivity, measured as the number of functional links between green patches, where each pair of patches was connected by ≤ 5 m of cleared land, negatively influenced insect density, possibly because increasing connectivity may strengthen emigration from local patches (Su *et al.* 2015). Thus, out of 11 studies which dealt with the effect of isolation, 7 (64%) supported Prediction 3, and 3 (36%) did not. Isolation also affects arthropod community structure in urban green spaces, as for butterflies in Palo Alto (Blair & Launer 1997), and in south east Finland (Saarinen *et al.* 2005, Valtonen *et al.* 2007), for

287   orthopterans and cicadellids in Bremen and Berlin (Strauss & Biedermann 2006), and forest

288   carabids in Brussels (Gaublomme *et al.* 2008). The influence of the habitat quality and urban matrix

289   is however complex and a study on the bumble bees in San Francisco parks indicated that park area,

290   distance to the nearest source population, and perimeter:area ratio did not predict bumble bee

291   community structure, whereas openness of the surrounding matrix and abundance of the dominant

292   competitor did (McFrederick & LeBuhn 2006).

293   For tenebrionids in Rome, in accordance with Prediction 7**,** early (pre-1960) extinctions were

294   promoted by increasing mean distance between green spaces, which suggests that increasing

295   isolation had a detrimental effect on species persistence (Fattorini 2014b). Isolation can have a

296   reduced impact also for very mobile species, but for opposite reasons. In this case, even green

297   spaces that are relatively far from each other can be easily reached. For example, carabids and

298   butterflies in Birmingham are able to disperse even across inhospitable environments to reach

299   isolated habitat-islands and are therefore more affected by habitat quality than isolation (Angold *et*

300   *al.* 2006). Small urban gardens in the heart of New York City host about 13% of the bee fauna of the

301   entire New York State area (Matteson *et al.* 2008). In Westchester County (a suburban area

302   immediately north of New York City), residential gardens host about 30% of the species recorded

303   for New York State (Fetridge *et al.* 2008).

304   As regards the urban-rural gradient, many studies identified a negative trend (e.g. Sadler *et al.*

305   2006; Jones & Leather 2012; New 2015 for reviews), which is consistent with Predictions 3 and 7.

306   However, other studies found a peak of insect species richness at the gradient mid-point (e.g. Blair

307   & Launer 1997; Marzluff 2005; Jones & Leather 2012; New 2015 for reviews). Most studies

308   regarding insects have dealt with carabid beetles, butterflies and hymenopterans, with patterns

309   varying according to the ecology of the concerned group (New 2015). No urban-rural gradient

310   effect was found for Rome tenebrionids (Fattorini 2014a), possibly because these insects include

311   both species associated with arid and sandy soils (which can be considered urban avoiders), and

312   species associated with ruderal and archaeological sites (which can be considered urban adapters).

313   Also, there is indication that biodiversity patterns along the urban-rural gradient are scale dependent

314   because of the irregular distribution of key resources or other biotope elements along gradients

315   (Hogsden & Hutchinson 2004).

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318   **DISCUSSION**

319   The species-area relationship (SAR) is one of the best documented patterns in island biogeography

320   (e.g. Lomolino *et al.* 2010). Although many exceptions exist, the majority of the urban studies that

321   we have reviewed report patterns that are consistent with the SAR (see also Nielsen *et al*. 2014),

322 possibly suggesting that larger green spaces should be preferred to smaller spaces (everything else

323 being equal). This may be an important point, because there is a debate whether a single larger

324 reserve should be preferred to several small areas (e.g. Fattorini 2010). However, if the final goal is

325 to preserve as many species as possible, and the total area that can be preserved is a fixed amount,

326 the idea that a single large reserve should be preferred to several small reserves may be questioned.

327 For example, giving preference to larger reserves might lead to faster disease spread, or may expose

328 species to local extinction in case of catastrophic events. In fact, when even the largest areas are

329 small (as in the case of most urban green spaces) and species distribution within the city is highly

330 fragmented, a network of many small spaces may be preferable to a few larger spaces. For example,

331 the tenebrionid beetles of Rome (Fattorini 2014b) revealed that, except for distance to other sites,

332 no significant correlation was found between conservation values of tenebrionid communities of

333 green spaces and site characteristics, thus suggesting that the conservation importance of urban

334 green spaces cannot be predicted on the basis of their geographical characteristics, but it must be

335 established on the basis of the species that they actually host.

336   In the case of urban green spaces, much attention has been focused on the importance of

337 extent and quality of forests as native habitat for animal conservation in urban areas (Andrén 1994;

338 Fahrig 1997; Donnelly & Marzluff 2004). However, the present analysis shows little support for this

339 claim. This result warns against the risk of generalizations about the conservation importance of

340 particular 'key habitats' and calls for studies that take into account local ecological settings and

341 species characteristics.

342   In general, urban green spaces tend to deviate substantially from a circular shape, being either

343 elongated or indented. Because of constraints imposed by the architecture of built-up areas, it is

344 virtually impossible to modify the shape of already existing urban green spaces. Thus, very limited

345 support for the importance of circular shapes sounds like good news. Because circularization is

346 inversely related to ecotonal development, this result may be explained by assuming that ecotonal

347 development may have negative effects on interior forest species, but a positive effect on open-

348 habitat and forest generalist species (Magura *et al.* 2001).

349   There is relatively strong support for the importance of connectivity. Most studies of insect

350 conservation in urban areas assumed that the matrix is wholly hostile and inhospitable, at least for

351 most of the native, non-synanthropic species. However, the urban matrix is not uniform, for

352 example because of the different intensity of development, and many insects can use resources from

353 regions beyond their immediate habitat patch (Dennis 2010). In general, the urban matrix isolating

354 green spaces is expected to be less hostile (i.e. easier to be crossed) than water for oceanic island

355 colonization. First, oceanic islands are typically very far from the mainland (hundreds or thousands

356 of kilometres), whereas urban green spaces are isolated from source areas by few kilometres or even

357   meters. Second, sea water is a strong barrier for most land animals (Cox & Moore 2010), especially

358   for those that disperse by walking and for which island colonization can occur only by passive

359   dispersal. Although crossing the urban matrix may be very hazardous, terrestrial, flightless insects

360   may move relatively easily among urban green spaces by active dispersal. Also, matrix permeability

361   is a function of species ecology, and response of arthropod species to isolation depends on their

362   ability to cross the matrix. Thus, promoting connectivity among urban green spaces by corridors or

363   a network of even very small spaces that may act as stepping stones may be a useful strategy for

364   insect conservation (New 2015).

365   In general, a variable number of case studies provided valuable insights to evaluate support

366   for Predictions 1-4. These predictions deal with patterns consistent with the ETIB, but not with the

367   underlying processes. We have identified, for each of these patterns, the possible underlying

368   processes on the basis of the ETIB (Prections 5-8), but we found a virtually complete lack of studies

369   that contained results useful to evaluate these postulated processes. In fact, despite the immense

370   literature on the ETIB, very few studies explicitly test the mechanisms by recording extinction and

371   colonization rates and the associated species turnover, especially over long periods (Wilson &

372   Simberloff 1968; Rey, 1981; Robinson *et al.* 1994; Burns & Neufeld 2009; Morrison 2010),

373   probably because of the lack of reliable biological data. Even in the paradigmatic case of the

374   Krakatau islands, Whittaker *et al.* (2000) suggested great caution in interpreting colonization and

375   extinction rates because the use of a limited data set led to an over-estimation of the extinction rates.

376   Progress in urban ecology will promote the use of urban green spaces not only to test patterns of

377   island biogeography, but also to explicitely test the underlying mechanisms, and better understand

378   implications for environmental conservation.

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381   **CONCLUDING REMARKS**

382   Island biogeography may continue to offer an important framework for urban ecology studies by

383   providing explicit and testable hypotheses. When applied to oceanic islands, the ETIB is too

384   simplistic for adequately capturing the diversity of patterns and processes that involve species with

385   different ecology and island systems that vary in their geographical, historical, and environemntal

386   characteristics (Lomolino *et al.* 2010). Yet, the ETIB still provides and will continue to provide

387   insights for understanding biogeographical phenomena in island biology and it may represent a

388   useful framework for urban ecology research as well.

389   Recent developments in island biogeography have been prompted by studies in species co-

390   occurrence and nestedness (Lomolino *et al.* 2010). Quite surprisingly, there is virtually no research

391   dealing with co-occurrence and nestedness patterns in urban areas. We think that future co-

392 occurrence and nestedness analyses would provide important insights not only into urban ecology

393 but also into island biogeography.

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612

Figure 1. Conceptual representation of predictions about variation in insect species richness of
urban green spaces. Species richness is expected to increase with increasing area, circularization,
connectivity (i.e. presence of corridors or proximity to other green spaces or rural areas) and extent
of natural habitats.
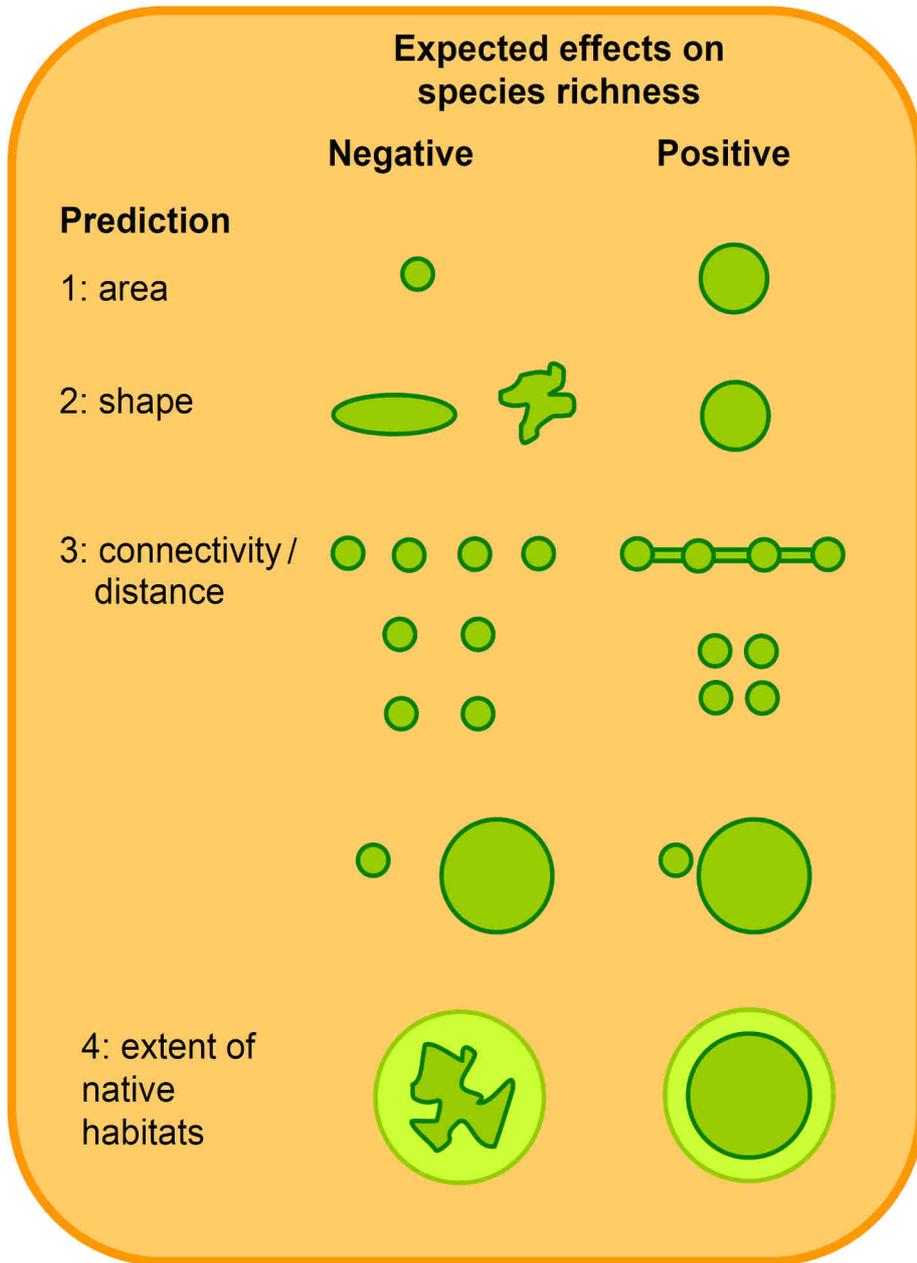
Figure 2. Number of case studies supporting or rejecting hypotheses about the influence of geographical characteristics of green spaces on insect species richness. Prediction 1: species richness is positively related to green space size; Prediction 2: a more circular shape increases species richness; Prediction 3: increasing isolation affects negatively species richness; Prediction 4: increasing extent of native habitats increases species richness.
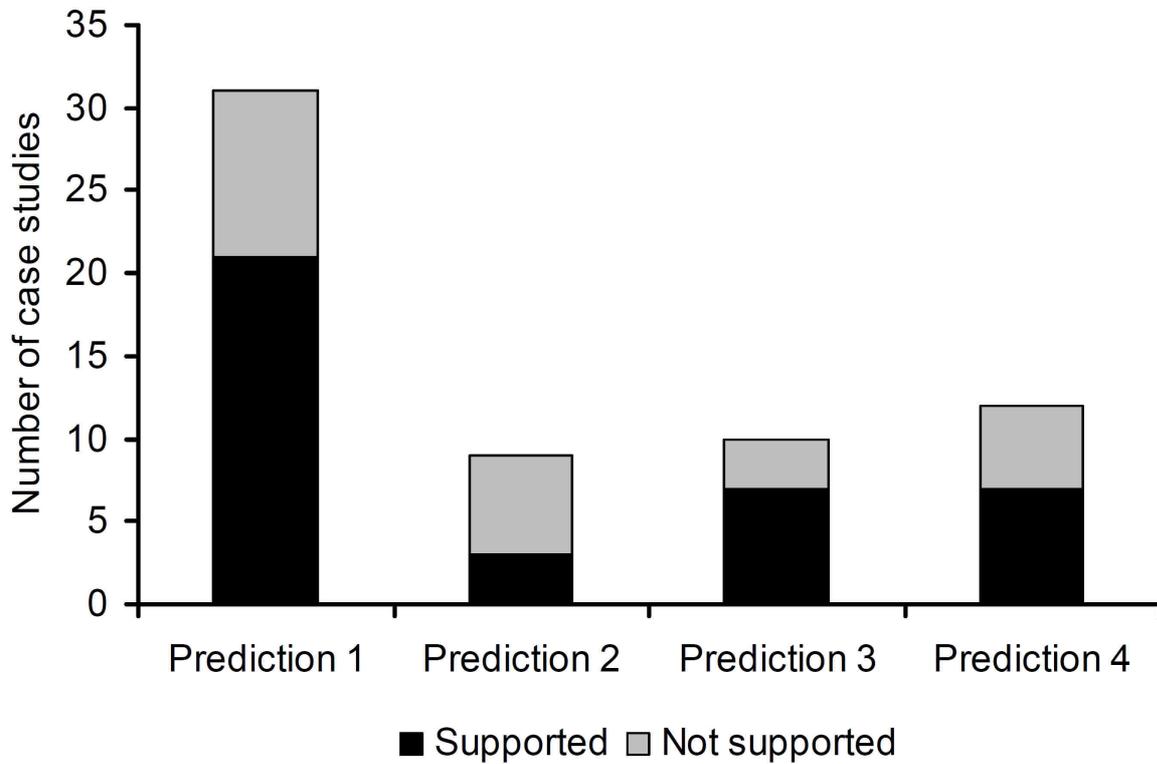
Table 1. Studies addressing predictions about insect species richness in urban green spaces.

Prediction	Studies that support the prediction	Studies that do not support the prediction	Level of support in literature
1 Species richness should increase with area	Faeth & Kane 1978; Bolger *et al.* 2000; Yamaguchi 2004; Koivula & Vermeulen 2005; Leather & Helden 2005; Saarinen *et al.* 2005; Pacheco & Vasconcelos 2007; Knap *et al.* 2008; Yamaura *et al.* 2008; Alvarenga *et al.* 2010; Bräuniger *et al.* 2010; Matteson & Langellotto 2010; Shwartz *et al.* 2013; Soga *et al.* 2013; Bod & Maciejewski 2014; Fattorini 2014	Bolger *et al.* 2000; Gaublomme *et al.* 2008; Koh & Sodhi 2004; Weller & Ganzhorn 2004; McFrederick & LeBuhn 2006; Smith *et al.* 2006; Clarke *et al.* 2008; Knap *et al.* 2008; Öckinger *et al.* 2009; Bräuniger *et al.* 2010; Matteson & Langellotto 2010; Lizée *et al.* 2012	Strong
2 Species richness should increase with circularisation of area shape	Bräuniger *et al.* 2010 ; Soga *et al.* 2013; Su *et al.* 2015	Koh & Sodhi 2004; McFrederick & LeBuhn 2006; Clarke *et al.* 2008 ; Yamaura *et al.* 2008; Öckinger & Smith 2009; Fattorini 2014b	Poor
3 Species richness should be inversely related to isolation	Davis 1979; Hardy & Dennis 1999; Magura *et al.* 2001; Koh & Sodhi 2004; Weller & Ganzhorn 2004; Pacheco & Vasconcelos 2007; Öckinger *et al.* 2009; Lizée *et al.* 2012	Öckinger *et al.* 2009; Bräuniger *et al.* 2010; Fattorini 2014b	Relatively strong
4 Species richness should increase with the extent of native habitats within each green space	Schiller & Horn 1997; Wolf & Gibbs 2004; Clarke *et al*. 2008; Bräuniger *et al.* 2010; Heneghan *et al.* 2012; Kotze *et al.* 2012; Breuste *et al.* 2013	Koh & Sodhi 2004; Pacheco &Vasconcelos 2007; Öckinger *et al.* 2009; Bräuniger *et a*l. 2010; Fattorini 2014a	Moderate