

1 **Global hotspots and correlates of alien species richness across taxonomic**  
2 **groups**

3 Wayne Dawson<sup>1\*</sup>, Dietmar Moser<sup>2</sup>, Mark van Kleunen<sup>3,4</sup>, Holger Kreft<sup>5</sup>, Jan Pergl<sup>6</sup>, Petr  
4 Pyšek<sup>6,7,8</sup>, Patrick Weigelt<sup>5</sup>, Marten Winter<sup>9</sup>, Bernd Lenzner<sup>2</sup>, Tim M. Blackburn<sup>10,11,12</sup>, Ellie E.  
5 Dyer<sup>10</sup>, Phillip Cassey<sup>13</sup>, Sally L. Scrivens<sup>13</sup>, Evan P. Economo<sup>14</sup>, Benoit Guénard<sup>15</sup>, César  
6 Capinha<sup>16,17</sup>, Hanno Seebens<sup>18</sup>, Pablo García-Díaz<sup>13,19</sup>, Wolfgang Nentwig<sup>20</sup>, Emili García-  
7 Berthou<sup>21</sup>, Christine Casal<sup>22</sup>, Nicholas E. Mandrak<sup>23</sup>, Pam Fuller<sup>24</sup>, Carsten Meyer<sup>25</sup> & Franz  
8 Essl<sup>2,8</sup>

9 <sup>1</sup>Department of Biosciences, Durham University, South Road, Durham, DH1 3LE, United  
10 Kingdom

11 <sup>2</sup>Division of Conservation Biology, Vegetation and Landscape Ecology, University Vienna,  
12 Rennweg 14, A-1030 Vienna, Austria

13 <sup>3</sup>Ecology, Department of Biology, University of Konstanz, Universitätsstrasse 10, Konstanz, D-  
14 78457, Germany

15 <sup>4</sup>Zhejiang Provincial Key Laboratory of Plant Evolutionary Ecology and Conservation, Taizhou  
16 University, Taizhou 318000, China

17 <sup>5</sup>Biodiversity, Macroecology & Biogeography, University of Goettingen, Büsgenweg 1, D-37077  
18 Göttingen, Germany

19 <sup>6</sup>Institute of Botany, Department of Invasion Ecology, The Czech Academy of Sciences, CZ-  
20 25243 Průhonice, Czech Republic

21 <sup>7</sup>Department of Ecology, Faculty of Science, Charles University, Viničná 7, CZ-12844 Prague,  
22 Czech Republic

23 <sup>8</sup>Centre for Invasion Biology, Department of Botany and Zoology, Stellenbosch University,  
24 Private Bag X1, Matieland 7602, South Africa

25 <sup>9</sup>German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Deutscher Platz  
26 5e, D-04103 Leipzig, Germany

27 <sup>10</sup>Centre for Biodiversity and Environment Research, Department of Genetics, Evolution and  
28 Environment, University College London, Gower Street, London, WC1E 6BT, United Kingdom

29 <sup>11</sup>Institute of Zoology, Zoological Society of London, Regent's Park, London, NW1 4RY, United  
30 Kingdom

31 <sup>12</sup>School of Biological Sciences, University of Adelaide, Adelaide, South Australia 5005,  
32 Australia

33 <sup>13</sup>School of Biological Sciences and Centre for Conservation Science and Technology (CCoST),  
34 The University of Adelaide, North Terrace SA 5005, Australia

35 <sup>14</sup>Okinawa Institute of Science and Technology Graduate University, 1919-1 Tancha, Onna,  
36 Okinawa, 904-0495, Japan

37 <sup>15</sup>School of Biological Sciences, The University of Hong Kong, Kadoorie Biological Sciences  
38 Building, Pok Fu Lam Road, Hong Kong SAR, China

39 <sup>16</sup>CIBIO/InBIO, Centro de Investigação em Biodiversidade e Recursos Genéticos, Cátedra  
40 Infraestruturas de Portugal-Biodiversidade, Universidade do Porto, Campus Agrário de Vairão,  
41 P-4485-661 Vairão, Portugal

42 <sup>17</sup>Zoologisches Forschungsmuseum Alexander Koenig, Adenauerallee 160, D-53113 Bonn,  
43 Germany

44 <sup>18</sup>Senckenberg Biodiversity and Climate Research Centre (BiK-F), Senckenberganlage 25, D-  
45 60325 Frankfurt am Main, Germany

46 <sup>19</sup>Landcare Research, P.O. Box 69040, Lincoln 7640, New Zealand  
47

48 <sup>20</sup>Institute of Ecology and Evolution, University of Bern, Baltzerstrasse 6, CH-3012 Bern,  
49 Switzerland

50 <sup>21</sup>GRECO, Institute of Aquatic Ecology, University of Girona, 17003 Girona, Catalonia, Spain

51 <sup>22</sup>FishBase Information and Research Group, Inc., Khush Hall, International Rice Research  
52 Institute, Los Baños, Laguna, Philippines

53 <sup>23</sup>Department of Biological Sciences, University of Toronto, 1265 Military Trail, M1C 1A4  
54 Toronto, Ontario, Canada

55 <sup>24</sup>United States Geological Survey, Nonindigenous Aquatic Species Program, Wetlands and  
56 Aquatic Research Center, 7920 NW 71<sup>st</sup> Street, 32653 Gainesville, Florida, USA

57 <sup>25</sup>Macroecology & Society, German Centre for Integrative Biodiversity Research (iDiv) Halle-  
58 Jena-Leipzig, Deutscher Platz 5e, D-04103 Leipzig, Germany

59 \*Correspondence to: [wayne.dawson@durham.ac.uk](mailto:wayne.dawson@durham.ac.uk)

60 **Human-mediated transport beyond biogeographic barriers has led to the introduction and**  
61 **establishment of alien species in new regions worldwide. However, we lack a global picture**  
62 **of established alien species richness for multiple taxonomic groups. Here, we assess global**  
63 **patterns and potential drivers of established alien species richness across eight taxonomic**  
64 **groups (amphibians, ants, birds, freshwater fishes, mammals, vascular plants, reptiles and**  
65 **spiders) for 186 islands and 423 mainland regions. Hotspots of established alien species**  
66 **richness are predominantly island and coastal mainland regions. Regions with greater**  
67 **gross domestic product per capita, human population density, and area have higher**  
68 **established alien richness, with strongest effects emerging for islands. Ants and reptiles,**  
69 **birds and mammals, and vascular plants and spiders form pairs of taxonomic groups with**  
70 **the highest spatial congruence in established alien richness, but drivers explaining richness**  
71 **differ between the taxa in each pair. Across all taxonomic groups, our results highlight the**  
72 **need to prioritize prevention of further alien species introductions to island and coastal**  
73 **mainland regions globally.**

74       The transport of species across biogeographic barriers by humans is a key component of  
75 global environmental change<sup>1-3</sup>. Some of the species introduced to new regions will establish  
76 self-sustaining populations and, thus, become a persistent part of the local biota<sup>4</sup>. Numbers of  
77 these established alien species (hereafter EAS) are predicted to increase further as a result of  
78 increasing global trade, land-use intensification, urbanization and climate change<sup>5</sup>. Whilst  
79 patterns of EAS richness have been analysed for particular regions<sup>6-8</sup> and taxa<sup>9-13</sup> individually, we  
80 still lack a global synthesis across a broad range of taxonomic groups. Such a synthesis will be  
81 invaluable for identifying (i) geographical hotspots and coldspots of EAS richness, both across

82 and within taxonomic groups, and for (ii) identifying and assessing potential correlates and  
83 drivers of EAS richness across different taxonomic groups

84 Here, we assess global patterns and correlates of EAS richness across eight taxonomic  
85 groups by integrating comprehensive published (vascular plants<sup>12</sup>, birds<sup>13</sup>, fishes<sup>14</sup>, ants<sup>15</sup>,  
86 spiders<sup>16</sup>) and so far unpublished databases (amphibians, mammals, reptiles) (Fig. 1). As a  
87 spatial framework, we use the 609 regions (186 islands/archipelagos and 423 mainland regions)  
88 from level 4 of the Biodiversity Information Standards framework (TDWG)<sup>17</sup>, representing  
89 countries or states and provinces within larger countries, and major islands and archipelagos. We  
90 identify the global hotspots (high richness) and coldspots (low richness) of EAS across the  
91 taxonomic groups while accounting for differences in area and sampling effort. Sampling effort  
92 consists of published inventory completeness estimates of native species of amphibians, birds  
93 and mammals<sup>18</sup>, vascular plants<sup>19</sup> and native genera of ants<sup>20</sup> as a proxy (see methods). We also  
94 explore additional macroecological and socioeconomic correlates behind cross-taxon EAS  
95 richness patterns.

96 We expect regions with higher gross domestic product per capita (GDPpc) or with higher  
97 population densities to receive more alien species introductions across taxa (i.e., to experience  
98 higher colonisation pressure through trade and transport), resulting in higher EAS richness<sup>7,8,10,21</sup>.  
99 We also test whether EAS richness patterns follow the latitudinal gradients often observed for  
100 native biota, with higher richness in regions with higher mean annual temperature and  
101 precipitation<sup>22,23</sup>. We expect island regions to have higher EAS richness than mainland regions,  
102 as islands are thought to be more prone to the establishment of alien species<sup>12,24,25</sup>. In addition,  
103 we expect more isolated oceanic islands to have greater EAS richness, as they have been shown  
104 to receive more introductions, at least for birds<sup>9</sup>. We also expect coastal regions (as points of

105 introduction) to have higher EAS richness than landlocked regions. Finally, we assess the degree  
106 of spatial congruence of EAS richness among taxonomic groups and explore the variables that  
107 might explain differences in spatial species-richness patterns among groups.

108

## 109 **Results**

### 110 *Established alien species richness and its drivers*

111 After accounting for area and sampling effort, hotspot regions for EAS richness across  
112 taxonomic groups are predominantly islands, with the top three regions being the Hawaiian  
113 Islands, New Zealand's North Island and the Lesser Sunda Islands (Indonesia) (Fig. 2;  
114 Supplementary Table 1). The top three coldspots are Antarctica (unsurprisingly), Coral Sea  
115 Island Territory (Australasia) and Laccadive Islands (Supplementary Table 1). Representation of  
116 continents differs markedly for regions above and below the richness median ( $\chi^2 = 16.34$ ,  $df = 8$ ,  
117  $P = 0.04$ ), with the Pacific Islands, Europe and Australasia represented disproportionately among  
118 higher-richness regions (Fig. 2; Supplementary Table 2). The model best explaining cross-taxon  
119 EAS richness for mainland and island regions includes GDPpc, population density and sampling  
120 effort, as well as area, mean annual precipitation, and whether a region is mainland or island(s)  
121 (Supplementary Table 3; Table 1). Following the (almost) universal species-area relationship for  
122 native species, larger regions have higher EAS richness, but regions with greater GDPpc, higher  
123 population density and greater sampling effort for native flora and fauna also have higher EAS  
124 richness (Table 1). The effects of climate are less pronounced than those of area, GDPpc and  
125 human population density, with a weak trend of higher alien richness in wetter regions (Table 1).  
126 While we only have potential proxy data (GDPpc, population density) for colonisation pressure  
127 here (i.e., the total numbers of species introduced)<sup>26</sup>, our results suggest that cumulative numbers

128 of EAS are driven to a greater extent by differences in area and the pressure of introductions  
129 from human history and activity<sup>1,3,5,12,21</sup> than by climate.

130 Island regions have on average higher cross-taxon EAS richness (mean  $\pm$  1 S.D.  
131 proportional cross-taxon richness =  $0.17 \pm 0.11$ ) than mainland regions (mean  $\pm$  1 S.D. =  $0.11 \pm$   
132  $0.07$ ; Table 1). In addition, models explaining alien richness of island and mainland regions  
133 separately reveal that EAS richness is more strongly related to area, GDPpc and population  
134 density on islands than in mainland regions (Table 1). Moreover, EAS richness is strongly  
135 related to mean annual temperature for islands, with warmer regions having higher richness,  
136 while the effect of mean annual temperature on mainland region richness was reversed, with  
137 cooler regions having higher richness (Table 1). Mainland regions with better sampled native  
138 species also harbour more EAS, but for island regions the effect of sampling effort is weaker  
139 (Table 1). Among mainland regions, EAS richness is greater for coastal (mean  $\pm$  1 S.D.  
140 proportional cross-taxon richness =  $0.13 \pm 0.09$ ) than for landlocked regions (mean  $\pm$  1 S.D. =  
141  $0.10 \pm 0.04$ ). Cross-taxon EAS richness on islands tends to be higher for those further from  
142 continental landmasses (Table 1).

143

#### 144 *Taxonomic congruence*

145 The strongest correlations in alien richness between taxonomic groups exist for ants and  
146 reptiles ( $r_s = 0.62$ ), followed by birds and mammals, and vascular plants and spiders (both  $r_s =$   
147  $0.55$ ) (Table 2). For ants and reptiles, EAS richness is high in the Hawaiian Islands, southern  
148 United States (especially Florida) and Madagascar and the Mascarene Islands (Fig. 1b, 1g).  
149 Mammals and birds both have high EAS richness in New Zealand, Hawaiian Islands, Florida and  
150 California, and are less congruent in Australia, Western Europe and the Caribbean (Figure 1c,

151 1e). Alaska, British Columbia and southern Africa tend to have high EAS richness of mammals,  
152 but not birds (Figure 1c, 1e). Plants and spiders both have high EAS richness in Hawaii,  
153 California and Florida, but are less congruent in other coastal regions of the USA and Canada,  
154 and in Australia (Fig. 1f, 1h). In Europe, the United Kingdom has the highest established alien  
155 plant richness, while Germany has the highest spider richness (Fig. 1h, 1h). Overall, the  
156 Hawaiian Islands, California, Florida and Australasian regions stand out as having high EAS  
157 richness for multiple taxonomic groups (Fig. 1).

158         The strong correlation in EAS richness between ants and reptiles is reflected in the  
159 positive relationship between mean annual temperature and EAS richness of these two  
160 taxonomic groups (Fig. 3). For both plants and spiders, human population density shows a strong  
161 positive relationship with EAS richness. However, the effects of socioeconomic and  
162 macroecological drivers on EAS richness differ markedly between birds and mammals despite  
163 the strong correlation between them, with stronger sampling effort effects for birds (Fig. 3). In  
164 addition, EAS richness of fishes, mammals and plants is negatively related to mean annual  
165 temperature, despite the relatively weak correlations among them (Fig. 3; Table 2). All other  
166 drivers included in best-fitting (lowest AICc) models for each taxonomic group have a positive  
167 relationship with EAS richness (Fig. 3).

168

## 169 **Discussion**

170         Our results show that, per unit increase in area, GDPpc, and population density, EAS  
171 richness increases at a faster rate in island than in mainland regions. A potential reason may be  
172 that island regions are more readily invaded by alien species than mainland regions<sup>25</sup>, although a  
173 rigorous test of this explanation would require data on failed introductions<sup>26</sup>. The opposing



174 relationships between mean annual temperature and richness for island and mainland regions  
175 may result from geographical bias in human activities for islands. Many economically  
176 independent island states are tropical, and may have high foreign import volumes (and thus high  
177 colonisation pressure), whereas most non-tropical islands are part of larger mainland states, with  
178 presumably limited foreign trade (and thus low colonisation pressure). The opposite may explain  
179 the lower EAS richness in tropical mainland regions, which have smaller trade volumes than  
180 temperate mainland regions<sup>5</sup>. Higher EAS richness in coastal than landlocked mainland regions  
181 is likely to be a consequence of the presence of ports in coastal regions<sup>1</sup>, resulting in overall  
182 greater rates of species introductions, as previously shown globally for birds<sup>13</sup> and for multiple  
183 aquatic species in the UK and Ireland<sup>27</sup>. Despite these effects, substantially more variation (20-  
184 26% more) in EAS richness is explained when also accounting for continent and subcontinent  
185 effects (marginal vs. conditional  $R^2$ , Table 1). This indicates that EAS richness may be further  
186 driven by spatially correlated socioeconomic, historical or political factors not captured by the  
187 variables analysed here. For example, some countries with high per-capita GDP have recently  
188 adopted biosecurity regulations to prevent introductions<sup>13</sup>, while the global spread of the tropical  
189 fire ant (*Solenopsis geminata*) originates from accidental introductions during European  
190 colonialism<sup>28</sup>. Such historical and political effects will drive fine-scale variation in colonisation  
191 pressure<sup>26</sup>, which has been shown to be the strongest determinant of alien bird species richness  
192 globally<sup>13</sup>, and for which the socioeconomic information used here may not be a strong proxy.

193         The moderate-to-strong correlations in EAS richness between birds and mammals, plants  
194 and spiders, and ants and reptiles may indicate that EAS richness patterns of these pairs of taxa  
195 share similar underlying drivers. Indeed, the models best explaining ant and reptile richness  
196 include strong positive effects of mean annual temperature on alien richness (Fig. 3). The

197 correlation between plant and spider richness may reflect horticulture and fruit/vegetable imports  
198 acting as major pathways of accidental introductions for both groups<sup>29</sup>. Human population  
199 density has similarly strong effects on richness for plants and spiders, but also for fishes,  
200 potentially reflecting a greater number of introductions for these groups that have occurred in  
201 more densely populated regions (Fig. 3).

202         However, spatial congruence of EAS richness may also result from different underlying  
203 drivers. For instance, mean annual temperature has a negative effect on established alien plant  
204 richness, but is not retained in the model for spider richness (Fig. 3). Similarly, while cooler  
205 regions have higher established alien mammal richness, possibly reflecting more frequent  
206 transfers of mammals between temperate regions<sup>30</sup>, temperature is unimportant for explaining  
207 established alien bird richness (Fig. 3) despite the strong congruence in the richness of these  
208 taxa. While some taxonomic groups show higher spatial congruence than others, no pairwise  
209 correlation is above 0.6, in contrast to native species richness<sup>31</sup>. This indicates that there is a  
210 substantial amount of spatial variation in EAS richness among groups (Fig. 1), and as such the  
211 effects of key macroecological and socioeconomic correlates will also vary (Fig. 3).

212         Sampling effort is much more strongly related to established alien bird than to mammal  
213 richness, despite their positive correlation (Fig. 3). Historical introductions of birds occurred  
214 through pet trade and Acclimatization Societies<sup>13,32,33</sup> and may be tightly linked to sampling  
215 effort (regions with the best record of native bird richness also tended to have more alien  
216 birds)<sup>13</sup>. Ultimately, completeness of regional inventories, and introduction and recording of  
217 alien species could be driven by similar historical, socioeconomic or cultural factors. For  
218 instance, regions that have channelled more resources towards creating a more complete record  
219 of native species may be the same ones importing and recording more alien species. However,

220 the extent to which current per-capita GDP and population density reflect colonisation pressure  
221 and sampling effort in the past is likely to differ among taxa.

222 Our global assessment of EAS richness and its correlates across eight different taxonomic  
223 groups reveals that island regions across the globe, relative to their size and sampling effort,  
224 harbour consistently more alien species than mainland regions. Densely populated islands with  
225 higher GDPpc and with warmer climates are particularly vulnerable. Coastal mainland regions  
226 also have higher EAS richness than landlocked ones. Island and coastal mainland regions may be  
227 alien species hotspots because colonisation pressure is higher, as has been shown for birds<sup>13</sup>, or  
228 because establishment rates among introduced alien species is higher in these regions. Across  
229 multiple taxa, it remains to be tested which of these two possibilities is more likely.  
230 Socioeconomic factors are clearly important for explaining EAS richness for all taxonomic  
231 groups, but effects vary depending on the group under study. This likely reflects differences  
232 among taxonomic groups in how well socioeconomic activity reflects colonisation pressure.  
233 Ultimately, data on the failed introductions, as well as the successful ones, will enable us further  
234 to understand global patterns in EAS richness. Nonetheless, the types of regions most vulnerable  
235 to EAS that we have identified should be considered priorities for efforts aimed at preventing  
236 further species introductions.

237

## 238 **References**

- 239 1. di Castri, F. in *Biological Invasions: a Global Perspective* (eds Drake, J. A., Mooney, H.,  
240 di Castri, F., Groves, R. H., Kruger, F. J., Rejmánek, M. & Williamson, M.) 1–30  
241 (Wiley, 1989).

- 242 2. Simberloff, D. *et al.* Impacts of biological invasions: what's what and the way forward.  
243 *Trends Ecol. Evol.* **28**, 58–66 (2013).
- 244 3. Lewis, S.L. & Maslin, M. A. Defining the Anthropocene. *Nature* **519**, 171–180 (2015).
- 245 4. Blackburn, T. M. *et al.* A proposed unified framework for biological invasions. *Trends*  
246 *Ecol. Evol.* **26**, 333–339 (2011).
- 247 5. Seebens, H. *et al.* Global trade will accelerate plant invasions in emerging economies  
248 under climate change. *Glob. Chang. Biol.* **21**, 4128–4140 (2015).
- 249 6. Poessel, S.A. Beard, K.H., Callahan, C.M., Ferreira, R.B. & Stevenson, E.T. Biotic  
250 acceptance in introduced amphibians and reptiles in Europe and North America. *Glob.*  
251 *Ecol. Biogeogr.* **22**, 192–201 (2013).
- 252 7. Essl, F. *et al.* Socioeconomic legacy yields and invasion debt. *Proc. Natl. Acad. Sci. USA*  
253 **108**, 203–207 (2011).
- 254 8. Jeschke, J.M & Genovesi, P. Do biodiversity and human impact influence the  
255 introduction or establishment of alien mammals? *Oikos* **120**, 57–64 (2011).
- 256 9. Blackburn, T.M., Cassey, P. & Lockwood, J.L. The island biogeography of exotic bird  
257 species. *Glob. Ecol. Biogeogr.* **17**, 246–251 (2008).
- 258 10. Capinha, C., Essl, F., Seebens, H., Moser, D. & Pereira, H.M. The dispersal of alien  
259 species redefines biogeography in the Anthropocene. *Science* **348**, 1248–1251 (2015).
- 260 11. Essl, F., Dullinger, S., Moser, D., Steinbauer, K. & Mang, T. Macroecology of global  
261 bryophyte invasions at different invasion stages. *Ecography* **38**, 488–498 (2015).

- 262 12. van Kleunen, M. *et al.* Global exchange and accumulation of non-native plants. *Nature*  
263 **525**, 100–103 (2015).
- 264 13. Dyer, E.E. *et al.* The global distribution and drivers of alien bird species richness. *PLoS*  
265 *Biol.* **15**, e2000942 (2017).
- 266 14. Froese, R. & D. Pauly (eds.) FishBase. [www.fishbase.org](http://www.fishbase.org), *version 09/2015* (2015)
- 267 15. Guénard, B., Weiser, M.D., Gomez, K., Narula, N. & Economo, E.P. The Global Ant  
268 Biodiversity Informatics (GABI) database: synthesizing data on ant species geographic  
269 distribution. *Myrmecological News* **24**: 83–89 (2017).
- 270 16. World Spider Catalog version 17.0, <http://wsc.nmbe.ch> (Natural History Museum Bern,  
271 2015).
- 272 17. Brummit, R. K. *World Geographical Scheme for Recording Plant Distributions Edition*  
273 *2*. (Hunt Institute for Botanical Documentation, Pittsburgh, 2001).
- 274 18. Meyer, C., Kreft, H., Guralnick, R. & Jetz, W. Global priorities for an effective  
275 information basis of biodiversity distributions. *Nat. Commun.* **6**, 8221 (2015).
- 276 19. Meyer, C., Weigelt, P. & Kreft, H. Multidimensional biases, gaps and uncertainties in  
277 global plant occurrence information. *Ecol. Lett.* **19**, 992–1006 (2016).
- 278 20. Guénard, B., Weiser, M.D. & Dunn, R.R. Global models of ant diversity suggest regions  
279 where new discoveries are most likely are under disproportionate deforestation threat.  
280 *PNAS* **109**, 7368–7373 (2012).
- 281 21. Pyšek, P. *et al.* Disentangling the role of environmental and human pressures on  
282 biological invasions across Europe. *PNAS* **107**, 12157–12162 (2010).

- 283 22. Gaston, K. J. Global patterns of biodiversity. *Nature* **405**, 220–227 (2000).
- 284 23. Lambdon, P. W. *et al.* Alien flora of Europe: species diversity, temporal trends,  
285 geographical patterns and research needs. *Preslia* **80**, 101–149 (2008).
- 286 24. Denslow, J.S. Weeds in paradise: thoughts on the invisibility of tropical islands. *Ann. Mo.*  
287 *Bot. Gard.* **90**, 119–127 (2003).
- 288 25. Lonsdale, W.M. Global patterns of plant invasions and the concept of invasibility.  
289 *Ecology* **80**, 1522–1536 (1999).
- 290 26. Lockwood, J.L., Cassey, P. & Blackburn, T.M. The more you introduce the more you  
291 get: the role of colonization pressure and propagule pressure in invasion ecology. *Divers.*  
292 *Distrib.* **15**, 904–910 (2009).
- 293 27. Gallardo, B. & Aldridge, D.C. The “dirty-dozen”: socio-economic factors amplify the  
294 invasion potential of 12 high-risk aquatic invasive species in Great Britain and Ireland. *J.*  
295 *Appl. Ecol.* **50**: 757–766 (2013).
- 296 28. Gotzek, D. *et al.* Global invasion history of the tropical fire ant: a stowaway on the first  
297 global trade routes. *Mol. Ecol.* **24**, 374–388 (2015).
- 298 29. Nentwig, W. Introduction, establishment rate, pathways and impact of spiders alien to  
299 Europe. *Biol. Invas.* **17**, 2757–2778 (2015).
- 300 30. Genovesi, P., Bacher, S., Kobelt, M., Pascal, M. & Scalera, R. in *Handbook of Alien*  
301 *Species in Europe* (eds DAISIE) 119–128 (Springer, 2009).
- 302 31. Qian, H. & Ricklefs, R.E. Global concordance in diversity patterns of vascular plants and  
303 terrestrial vertebrates. *Ecol. Lett.* **11**, 547–553 (2008).

- 304 32. Lever, C. in *Encyclopedia of Biological Invasions* (eds Simberloff, D. & Rejmánek, M.)  
305 1–4 (University of California Press, 2011).
- 306 33. Felemban, H. M. On the exotic birds imported into Jeddah, Saudi Arabia. *Zool. Middle*  
307 *East* **8**, 15–16 (1993).

308

309 **Acknowledgements** This research benefited from support from the European Commission  
310 (COST Action TD1209). The Deutsche Forschungsgemeinschaft supported H.S. (DFG, grant SE  
311 1891/2-1), M.v.K. (KL 1866/9-1) and M.W. (FZT 118), the Austrian Science Foundation  
312 supported F.E., B.L. and D.M. (FWF, grant I2096-B16). P.P. and J.P. were supported by the  
313 Academy of Sciences of the Czech Republic (no. RVO 67985939), Praemium Academiae award  
314 to P.P., and Czech Science Foundation (project no. 14-36079G). C.Cap. was supported by a  
315 postdoctoral grant from the Portuguese Foundation for Science and Technology (FCT/MCTES)  
316 and POPH/FSE (EC) grant SFRH/BPD/84422/2012. E.G.-B. was supported by the Spanish  
317 Ministry of Economy and Competitiveness (projects CGL2013-43822-R and CGL2015-69311-  
318 REDT). C.M. was supported by the Volkswagen Foundation through a Freigeist Fellowship.

319

320 **Author contributions** The GloNAF core team (M.v.K., P.P., W.D., F.E., J.P., M.W., H.K. and  
321 P.W.), T.B., H.S. and B.L. conceived the idea; W.D. coordinated data collation, and designed  
322 and led the analyses and writing with major inputs from F.E., D.M. M.v.K., P.P., H.K., M.W.,  
323 J.P., P.W., and further inputs from all other authors. Data were contributed by the GloNAF  
324 database for vascular plants, E.E. and B.G. for ants, C.Cap., F.E., H.S. and P.G.-D. for  
325 amphibians and reptiles, T.B. and E.D. for birds, C.Cas., E.G.-B., P.F. and N.M. for fishes, P.C.

326 and S-L.S for mammals, and W.N. for spiders. D.M. collected and calculated data on region area  
327 and sampling effort. C.M. contributed data on completeness of native species richness  
328 inventories.

329

330 **Author Information** Reprints and permissions information is available at  
331 [www.nature.com/reprints](http://www.nature.com/reprints). The authors declare no competing financial interests. Readers are  
332 welcome to comment on the online version of the paper. Correspondence and requests for  
333 materials should be addressed to W.D. ([wayne.dawson@durham.ac.uk](mailto:wayne.dawson@durham.ac.uk)).



334 **Figure 1 | Established alien species richness in the 609 TDWG level-4 regions with data**  
335 **available per taxonomic group.** a) amphibians, b) ants, c) birds, d) freshwater fishes, e)  
336 mammals, f) vascular plants, g) reptiles and h) spiders. Grey areas represent regions with no data  
337 available for a particular taxonomic group. Scales indicate numbers of species.

338

339 **Figure 2 | Hotspot and coldspot regions for cross-taxon established alien species richness**  
340 **across eight taxonomic groups (amphibians, ants, birds, freshwater fishes, mammals,**  
341 **vascular plants, reptiles and spiders), accounting for area and sampling effort.** Only TDWG  
342 level-4 regions (i.e. countries, federal states and islands/archipelagos) with data on sampling  
343 effort available were included ( $n=534$ ). Cross-taxon established alien species richness of grey-  
344 bordered regions was calculated from three or fewer taxonomic groups, and of black-bordered  
345 regions from four or more taxonomic groups. Cross-taxon established alien species richness  
346 comprises residuals from a linear model,  $\ln[\text{cross-taxon alien richness}] \sim \ln[\text{Area}] \times \text{sampling}$   
347  $\text{effort}$ . Upper and lower 2.5% and 10% regions are indicated separately from the remaining upper  
348 and lower 50% regions.

349

350 **Figure 3 | Effects of area, climate, sampling effort, GDP per capita, human population**  
351 **density and whether a region is coastal on established alien species richness of eight**  
352 **taxonomic groups (mainland regions only, due to insufficient data for islands for all**  
353 **taxonomic groups).** Estimates ( $\pm 1$  standard error) of effects were obtained from linear mixed  
354 effects models of  $\ln(\text{species richness}+1)$ , with regions, nested in subcontinental regions (TDWG  
355 level 2) and continents as random effects. Note that only variables that were kept in the final  
356 models are shown (Supplementary Table 6), thus numbers of estimates differ between groups.  
357 Numbers in parentheses are numbers of regions included per taxonomic group.

358 **Table 1 | Estimates of models explaining cross-taxon established alien species richness for**  
359 **all regions, and for mainland or island regions only.** Cross-taxon alien richness was natural-  
360 log transformed, as were GDP per capita (thousands \$US), human population density ( $10^3$  people  
361  $\text{km}^{-2}$ ) and region area ( $\text{km}^2$ ). Mean annual precipitation (MAP) was square-root transformed.  
362 Standard errors are in parentheses. Random effects of TDWG level 2 regions and continents and  
363 residual variation (*italics*) are shown as 1 standard deviation. Shaded cells indicate when a  
364 variable was not considered. Marginal  $R^2$  (variation explained by fixed effects) and conditional  
365  $R^2$  (fixed and random effects) are also given.

366

	All regions	Mainland	Island
<i>N</i>	446	371	75
Intercept	-1.74 (0.08)	-2.32 (0.05)	-1.92 (0.10)
Area	0.35 (0.03)	0.25 (0.02)	0.53 (0.07)
Sampling Effort	0.17 (0.03)	0.17 (0.03)	0.10 (0.06)
Area × Sampling Effort	0.07 (0.02)	0.08 (0.01)	
Mainland	-0.44 (0.07)		
Coastal		0.13 (0.03)	
Distance to continent			0.18 (0.07)
MAT		-0.08 (0.03)	0.25 (0.10)
MAP	0.06 (0.02)	0.06 (0.02)	
GDP per capita	0.19 (0.03)	0.12 (0.03)	0.31 (0.07)
Human Population density	0.23 (0.02)	0.19 (0.03)	0.35 (0.07)
<i>TDWG continent</i>	<i>0.14</i>	<i>0.07</i>	<i>0.22</i>
<i>TDWG L2 region</i>	<i>0.24</i>	<i>0.20</i>	<i>0.31</i>
<i>Residual</i>	<i>0.30</i>	<i>0.26</i>	<i>0.40</i>
Marginal/Conditional $R^2$	0.45/0.71	0.49/0.69	0.58/0.79

367 **Table 2 | Established alien species richness correlations (Spearman's  $r_s$ ) between pairs of**  
 368 **the eight taxonomic groups, for all regions with data available. Significant ( $P < 0.05$ )**  
 369 correlations are indicated in bold.

	Ants	Amphibians	Mammals	Birds	Fishes	Plants	Spiders
Reptiles	<b>0.62</b>	<b>0.41</b>	<b>0.26</b>	<b>0.44</b>	<b>0.14</b>	<b>0.17</b>	<b>0.34</b>
Ants		<b>0.34</b>	0.10	<b>0.29</b>	<b>0.15</b>	0.06	<b>0.28</b>
Amphibians			<b>0.43</b>	<b>0.47</b>	<b>0.19</b>	<b>0.19</b>	<b>0.34</b>
Mammals				<b>0.55</b>	<b>0.23</b>	<b>0.32</b>	<b>0.36</b>
Birds					<b>0.34</b>	<b>0.39</b>	<b>0.46</b>
Fishes						<b>0.35</b>	<b>0.40</b>
Plants							<b>0.55</b>

370

371

372 **METHODS**

373 **Data compilation.** Data on established alien species (EAS) richness were obtained from  
374 databases for eight taxonomic groups (amphibians, ants, birds, mammals, vascular plants,  
375 reptiles, spiders). The data on amphibians, reptiles and spiders, and fishes in some regions were  
376 compiled specifically for this study. For all taxonomic groups, only EAS outside of their native  
377 ranges have been considered.

378 Data on alien vascular plants were obtained from the Global Naturalized Alien Flora  
379 database version 1.1<sup>12</sup>, a recently compiled database including 13,168 plant species (including  
380 hybrids and subspecies). The data consists of lists of established alien plant species in 843  
381 geopolitical regions, largely conforming to countries, states, provinces and counties within  
382 countries, as well as islands and archipelagos. Data on established alien ants were obtained from  
383 the Global Ant Biodiversity Informatics project database, which consists of geographical records  
384 of species' presences (accessible through antmaps.org<sup>15</sup>). Only species records representing  
385 establishment in the wild (e.g. not in glasshouses or buildings) were included, amounting to 4061  
386 records for 237 species in total. Data on established alien bird species were obtained from the  
387 Global Avian Invasions Atlas<sup>31</sup>, which is a comprehensive global database of 971 alien bird  
388 species with 27,723 introduction records at a 1-degree grid-cell resolution. Data on 445  
389 established alien mammal species were obtained from a geographically complete mammal  
390 database (Alien Mammal Data v1.0), which contains records of established alien mammal  
391 species in global administrative areas (GADM; www.gadm.org). Data on 81 established alien  
392 amphibian and 203 established alien reptile species were compiled from multiple sources into a  
393 database, the Global Alien Amphibians and Reptiles Database, by Capinha, Essl and Seebens  
394 specifically for the purpose of this study, and merged with a separate database compiled by  
395 García-Díaz. Data on 454 established alien freshwater fish species (including migratory species

396 with marine life-stages, a total of 2968 records) were taken from the FishBase database<sup>14</sup>  
397 (accessed 13<sup>th</sup> of October 2015), and supplemented for the U.S.A. with the U.S. Geological  
398 Survey's Nonindigenous Aquatic Species database (compiled by Fuller), Canada (compiled by  
399 Mandrak), multiple sources for Mexico<sup>32</sup>, Argentinian, Chilean, Australian, New Zealand<sup>33,34</sup>  
400 and South African provinces (compiled by García-Berthou)<sup>35,36</sup>, Japan<sup>37</sup> and Brazil<sup>38</sup>. Finally,  
401 2138 records on 207 established alien spider species were compiled via a comprehensive  
402 literature search by Nentwig, including the World Spider Catalog<sup>16</sup> as a major source, and  
403 literature available therein.

404 Because the data for the different taxonomic groups came from different sources and were  
405 originally collected at different spatial resolutions, we harmonised all data sets to fit within the  
406 Biodiversity Information standards (TDWG) geographic system<sup>17</sup>. This hierarchical system  
407 includes as the finest spatial resolution (Level 4) a layer of 609 regions, mostly comprising  
408 countries, states and provinces of larger countries and major island groups. Species records for  
409 each taxonomic group were assigned to TDWG level 4 regions, and the total number of EAS per  
410 taxonomic group within each region was calculated. Global data coverage was highest for birds  
411 and mammals (both have all 609 regions), followed by vascular plants (449 regions, 82% of  
412 global ice-free terrestrial area), ants (402 regions, 64% of area), freshwater fishes (363 regions,  
413 70% of area), spiders (348 regions, 66% of area) and, lastly, amphibians and reptiles (311 and  
414 310 regions, 48% and 47% of area, respectively).

415

416 **Estimating sampling effort.** Variation in sampling of EAS among regions can bias the  
417 perceived global patterns in alien species richness. However, data directly measuring the degree  
418 of sampling effort of EAS recorded in each region are not available. To account for this potential

419 bias, we instead estimated sampling effort for native species of five taxonomic groups:  
420 amphibians, ants, birds, mammals and vascular plants. For amphibians, birds and mammals, we  
421 obtained global data at a 12321 km<sup>2</sup> (~1 degree) grid cell resolution, comprising the percentage  
422 completeness of native species inventories for these groups based on occurrence records  
423 mobilized *via* the Global Biodiversity Information Facility (GBIF)<sup>18</sup>. For vascular plants, we  
424 obtained data<sup>19</sup> at the same resolution comprising the percentage completeness of species records  
425 in GBIF, as assessed through comparison with independent estimates of native vascular plant  
426 richness. For ants, we used region estimates of the percentage of native ant genera missing from  
427 records in the Global Ant Biodiversity Informatics project database (these estimates were  
428 obtained from models predicting ant diversity and endemism, and region completeness was  
429 calculated as 100 per cent minus the percentage of missing genera)<sup>20</sup>. We then calculated the  
430 average completeness across grid cells for each TDWG level 4 region large enough to overlay  
431 the majority of at least one grid cell (534 regions in total: completeness could not be calculated  
432 for 64 island and 11 mainland regions). An average completeness value across the five  
433 taxonomic groups was then calculated per region, and used in subsequent analyses of cross-taxon  
434 alien richness (see below; Supplementary Fig. 1). When a taxonomic group had native  
435 completeness data available, this was used in the single taxon analyses (see below). Correlations  
436 between completeness values for individual taxonomic groups are all significantly positive  
437 (Supplementary Table 4), and as vertebrates, invertebrates and vascular plants are included, we  
438 are confident that the average completeness across these groups is broadly representative of the  
439 missing three taxonomic groups.

440 Our use of native species inventories as a proxy for sampling effort of EAS recording  
441 assumes there is a linear positive relationship between sampling efforts of alien and of native

442 species. However, the completeness measures are based on data sources which also include  
443 records of alien species, and we have no reason to believe that addition of EAS records will  
444 differ spatially in a fundamentally different way from native species records. By focusing our  
445 sampling effort estimates on native species, we ensure greater statistical independence between  
446 the estimates of EAS richness and sampling effort. In addition, completeness of regional  
447 inventories and recording of EAS could be driven by ultimately the same factors, such as human  
448 history, socioeconomy and culture. So we may expect certain regions to have more resources  
449 channelled towards creating a more complete recording of not only native species, but also to be  
450 introducing and recording more alien species.

451

452 **Cross-taxon established alien richness.** Species-richness values per region varied greatly  
453 among taxonomic groups (Fig. 1), making direct calculation of mean cross-taxon alien richness  
454 non-informative. Therefore, alien richness was converted to a relative richness scale, ranging  
455 from 0 to 1, for each taxonomic group, calculated as the regional species richness divided by the  
456 maximum richness for a given taxonomic group. The cross-taxon EAS richness for each region  
457 was then calculated as the mean of relative richness values across taxonomic groups. The  
458 number of taxonomic groups with data available per region ranged from two (46 regions) to the  
459 maximum of eight (145 regions), with a majority of regions (503) having four or more  
460 taxonomic groups.

461 As EAS richness of regions may depend on their area and the level of sampling effort in  
462 recording alien species, we also calculated a richness value correcting for these effects. This was  
463 achieved by fitting a linear model of  $\ln(\text{cross-taxon EAS richness})$  as a function of  $\ln(\text{area, km}^2)$ ,  
464 interacting with the sampling effort estimate (both variables were centred on their means and

465 scaled to their standard deviations). The interaction was included, as an effect of area may be  
466 more detectable for regions with greater sampling effort. Indeed, the interaction term was  
467 significant and positive (estimate [ $\pm$ SE]= 0.102 [0.030],  $F_{1,536} = 11.548$ ,  $P < 0.001$ ), as were the  
468 effects of area (estimate [ $\pm$ SE]= 0.156 [0.033],  $F_{1,536} = 15.582$ ,  $P < 0.001$ ) and sampling effort  
469 (estimate [ $\pm$ SE]= 0.178 [0.025],  $F_{1,536} = 53.888$ ,  $P < 0.001$ ) alone. This model explained 13% of  
470 variation in cross-taxon alien species richness, and a model that explicitly included the number  
471 of taxonomic groups as a weighting yielded very similar results. No regions with zero species  
472 across taxonomic groups were included due to a lack of data on sampling effort. The residuals  
473 from the non-weighted model were then extracted and used as area- and sampling effort-  
474 corrected, cross-taxon EAS richness for mapping and identifying hotspot regions.

475

#### 476 **Potential drivers of established alien species richness.**

477 We explored the ability of several variables to explain variation in cross-taxon EAS richness and  
478 richness of individual taxonomic groups. We calculated gross domestic product per capita  
479 (GDPpc) (in US dollars) for each TDWG level 4 region as the average of estimated values in 1  
480 km<sup>2</sup> grid cells, using estimates derived from night time light provided by Ghosh et al<sup>39</sup> .  
481 Population density in the year 2000 was calculated in a similar manner from 1 km<sup>2</sup> grid-cell  
482 values obtained from the Global Rural Urban Mapping Project (GRUMP;  
483 <http://sedac.ciesin.columbia.edu/data/set/grump-v1-population-density>). Mean annual  
484 temperature (MAT) and mean annual precipitation (MAP) were downloaded at 1 minute  
485 resolution from WORLDCLIM ([www.worldclim.org](http://www.worldclim.org); mean annual temperature = BIO1, and  
486 mean annual precipitation = BIO12 from the bioclim variables), and averages were calculated for  
487 each TDWG level 4 region. Area (km<sup>2</sup>) was calculated as geodesic area excluding permanent



488 ice-sheets, and each region was classified as being island (including archipelagoes) or mainland  
489 (part of a continental landmass; Greenland was coded as an island, Australia was treated as a  
490 continental landmass). Distance to mainland was calculated as the geodesic distance to the next  
491 continental land mass<sup>40</sup>. Mainland regions were further categorized as being coastal (i.e.  
492 bordering seas and/or oceans, not including the Caspian Sea) or landlocked.

493  
494 **Analyses.** In order to assess the correlates of cross-taxon EAS richness patterns across all  
495 regions, we used linear mixed models using the R package ‘nlme’<sup>40</sup> (ln-transformed, to satisfy  
496 assumptions of normality of residuals and variance homogeneity) as a function of the following  
497 fixed effects: area, sampling effort (average % native species completeness), and area interacting  
498 with sampling effort, gross domestic product per capita (GDPpc), population density, mean  
499 annual temperature, mean annual precipitation, and whether a region was a mainland or island  
500 region. Area, GDPpc and population density were ln-transformed, and mean annual precipitation  
501 was square-root transformed to linearize relationships with alien richness. We included the  
502 TDWG Level 2 subcontinental regions, nested within TDWG continents as random effects  
503 (random intercepts only). We also used the same model as above to model ln-transformed cross-  
504 taxon EAS richness for mainland and island regions separately, replacing the mainland-island  
505 status with, respectively, a binary variable describing mainland regions as landlocked or coastal,  
506 and with distance to the nearest continental landmass (km, square-root transformed) for island  
507 regions. We inspected Akaike’s Information Criterion corrected for small sample size (AICc) for  
508 all full models, and all models nested within them, to identify the set of models within 6 AICc  
509 units of the lowest-AIC model that best explain cross-taxon EAS richness for all regions, and for  
510 mainland and island regions separately (Supplementary Table 3). The lowest-AICc models

511 explaining richness across all regions, and for mainland and island regions only, were selected  
512 for inference, and marginal  $R^2$  (accounting for fixed effects) and conditional  $R^2$  (accounting for  
513 fixed and random effects) were calculated.

514 For individual taxonomic groups, we also ran linear mixed models as above to explain EAS  
515 richness ( $\ln[\text{number of species}+1]$  transformation). Due to insufficient data on sampling effort  
516 for several taxa in island regions, we restricted these analyses to mainland regions. Sampling  
517 effort for individual taxonomic groups and its interaction with area were included for  
518 amphibians, ants, birds, mammals and vascular plants. Sampling effort and its interaction with  
519 area was not included in models explaining fish, reptile and spider alien richness because data on  
520 native species inventory completeness were not available for these taxonomic groups.  
521 Information on model comparisons for individual taxon richness is summarized in  
522 Supplementary Table 5.

523 For all selected models, we checked for spatial autocorrelation of the residuals by  
524 constructing correlograms of Moran's  $I$  in relation to increasing distance (0 to 15000 km)  
525 between centroids of neighbouring regions. This was achieved using the 'spline.correlog'  
526 function in the R package 'ncf'<sup>42</sup>. To assess significance of spatial autocorrelation, a 95%  
527 confidence interval about Moran's  $I$  was constructed from 500 bootstrapped randomisations of  
528 the regions' residuals from the models. For models explaining cross-taxon EAS richness, there  
529 was a significant but only small amount of autocorrelation (Moran's  $I \leq 0.19$ ) when all regions or  
530 only mainland regions were considered, and only at very short distances between regions (<500  
531 km; Supplementary Fig. 2). For individual taxonomic groups, models showed a significant but  
532 small amount of autocorrelation at very short distances for only amphibians (Moran's  $I \leq 0.33$ ,

533 distance  $\leq$  650 km), birds (Moran's  $I \leq 0.23$ , distance  $\leq$  150 km), and freshwater fishes (Moran's  
534  $I \leq 0.30$ , distance  $\leq$  750 km) (Supplementary Fig. 3).

535

536 **Congruence in established alien species richness among taxonomic groups.** The strength of  
537 correlation in EAS richness between taxonomic groups was assessed by calculating Spearman  
538 correlation coefficients for every combination of pairs of taxonomic groups, using the actual  
539 species richness for each taxonomic group. The resulting number of regions used per pairwise  
540 correlation is shown in Supplementary Table 6. All analyses were conducted in R version 3.2.3<sup>43</sup>.

541

#### 542 **Data Availability Statement**

543 The dataset analysed in this study is available in Zenodo data repository,  
544 [<https://zenodo.org/record/556393#.WPjH08a1s2w>].

545

#### 546 **Conflict of Interest Statement**

547 The authors declare that no conflicts of interest have arisen through the production and  
548 publication of this article.

549

550 **References**

- 551 31. Dyer, E.E., Redding, D.W. & Blackburn, T.M. The Global Avian Invasions Atlas: A  
552 database of alien bird distributions worldwide. BIORXIV 090035 (2016).
- 553 32. Espinosa-Perez, H. & Ramirez, M. Exotic and invasive fishes in Mexico. *Check List*, **11**,  
554 1627 (2015).
- 555 33. McDowall, R.M. 2000: The Reed field guide to New Zealand freshwater fishes. Reed  
556 Publishing, New Zealand. 224 p
- 557 34. NIWA Atlas of NZ Freshwater Fishes  
558 <https://www.niwa.co.nz/freshwater-and-estuaries/nzffd/NIWA-fish-atlas>
- 559 35. Ellender, B.R. & Weyl, O.L.F. A review of current knowledge, risk and ecological  
560 impacts associated with non-native freshwater fish introductions in South Africa. *Aquat.*  
561 *Invasions* **9**:117–132 (2014).
- 562 36. Skelton, P.H. 2001. A Complete Guide to the Freshwater Fishes of Southern Africa.  
563 Southern Book Publishers, Cape Town, South Africa, 395 pp.
- 564 37. Invasive species of Japan database,  
565 [https://www.nies.go.jp/biodiversity/invasive/index\\_en.html](https://www.nies.go.jp/biodiversity/invasive/index_en.html), accessed 18 May, 2016  
566 (Environmental Risk Research Center, National Institute for Environmental Studies,  
567 Japan, 2016).
- 568 38. Brazil Invasive Alien Species Database, <http://i3n.institutohorus.org.br/www> – I3N,  
569 accessed 17 May 2016 (Florianopolis, Santa Catarina, Brazil, 2016).

- 570 39. Ghosh, T., Powell, R.L., Elvidge, C.D., Baugh, K.E., Sutton, P.C. & Anderson, S.  
571 Shedding light on the global distribution of economic activity. *The Open Geography*  
572 *Journal* **3**, 148–16 (2010).
- 573 40. Weigelt, P. & Kreft, H. Quantifying island isolation – insights from global patterns of  
574 insular plant species richness. *Ecography*, **36**, 417–429 (2013).
- 575 41. Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D. & R Core Team. nlme: Linear and  
576 nonlinear mixed effects models. R package version 3.1–128 (2016).
- 577 42. Bjornstad, O.N. ncf: Spatial nonparametric covariance functions. R package version 1.1-7  
578 (2016).
- 579 43. R Core Team. R: A language and environment for statistical computing (R Foundation  
580 for Statistical Computing, 2016).





