Defining and delivering resilient ecological networks: an example for nature conservation in England

Article

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1 **Defining and delivering resilient ecological networks: an example**

2 **for nature conservation in England**

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36 **Summary**

37   1. Planning for nature conservation has increasingly emphasised the concepts of

38   resilience and spatial networks. Although the importance of networks of habitat for

39   individual species is clear, their importance for long-term ecological resilience and

40   multi-species conservation strategies is less well established.

41   2. Referencing spatial network theory, we describe the conceptual basis for defining and

42   assessing a network of wildlife areas that supports the resilience of species to multiple

43   forms of perturbations and pressures. We explore actions that could enhance network

44   resilience at a range of scales, based on ecological principles, with reference to four

45   well-established strategies for intervention in a spatial network (Better, Bigger, More

46   and Joined) from the influential *Making Space for Nature* report by Lawton *et al.*

47   (2010).

48   3. Building existing theory into useable and scalable approaches applicable to large

49   numbers of species is challenging but tractable. We illustrate the policy context,

50   describe the elements of a long-term adaptive management plan and provide example

51   actions, metrics and targets for early implementation using England as a case study,

52   where there is an opportunity to include large-scale ecological planning in a newly

53   launched 25-year environment plan.

54   4. *Policy Implications*: The scientific principles to place resilience and network theory at

55   the heart of large-scale and long-term environmental planning are established and

56   ready to implement in practice. Delivering a resilient network to support nature

57   recovery is achievable, and can be integrated with ongoing conservation actions.

58   England's 25 Year Environment Plan provides the ideal testbed.

Introduction

62 It is well understood that species exhibit inter-connected dynamics over large areas ($>>10^3$

63 km^2). Metapopulation theory has been influential in applied ecology and conservation for

64 decades (Cadotte *et al.* 2017). Recent extensions of this concept to meta-communities and

65 networks of interlinked ecosystems (Logue *et al.* 2011; Pellissier *et al.* 2017) give rise to the

66 notion of spatial ecological networks, which describe the large-scale distribution and

67 dynamics of species and communities.

68 These dynamics are especially significant when considering longer-term resilience under

69 changing environmental pressures. There is now a substantial literature on ecological

70 resilience (Cumming & Peterson, 2017; Morecroft *et al.*, 2012; Oliver *et al.*, 2015). Here, we

71 define a resilient ecological network as one in which species can persist even in the face of

72 natural perturbations and human activities (including climate change). The twin concepts of

73 networks and resilience are becoming increasingly influential in conservation planning

74 (Albert *et al.* 2017; Bixler *et al.* 2016; Samways & Pryke, 2016), recognising both the current

75 pressures on biodiversity and future climate change. Designing, evidencing, and

76 implementing large-scale conservation plans to achieve resilient networks is increasingly

77 feasible, although conceptual and practical challenges remain.

78 We consider these challenges in the context of England, representing a region strongly

79 influenced by human activities. Lawton *et al.* (2010) concluded that England's wildlife sites

80 needed to be "Better", "Bigger", "More" and "Joined" (henceforth "BBMJ") to constitute a

81 resilient network. The Lawton report has been highly influential (Rose *et al.* 2016) but there

82 has been little progress towards realising it, partly reflecting a lack of clarity about what a

83 resilient ecological network would look like. The publication in January 2018 of a 25-year

84 environment plan (henceforth 25YEP) for England (DEFRA 2018) provides a focus to

85 synthesise scientific progress and an opportunity to put the Lawton vision into practice.

4

86   The 25YEP includes a goal to create a resilient Nature Recovery Network based on the

87   Lawton principles. Specific commitments include: creating 500,000 hectares of new wildlife

88   habitat; putting 75% of existing protected sites into 'favourable condition'; and developing

89   metrics to assess progress towards these goals (DEFRA 2018). However, it is unclear

90   whether delivering these commitments would be sufficient to achieve Lawton's vision of

91   enhanced biodiversity and functional ecosystems in the face of climate change and other

92   pressures.

93   In this paper, we explore the scientific basis for planning ecological networks that are

94   resilient, building on spatial network theory. We elaborate on the features of resilient

95   multispecies networks and the interventions required to support them. We then consider how

96   metrics of resilience might be developed with reference to the 25YEP. The practical

97   complexities involved in delivering and evidencing the 25YEP's goal will be challenging, but

98   we highlight immediate actions that would contribute to the goal with a low risk of

99   unintended consequences.

100   **The rationale for BBMJ**

101   Ecological networks are subject to numerous pressures, whose impact can be distinguished in

102   three ways: (i) specificity: whether a single site is affected, through to all sites in the network;

103   (ii) intensity: the magnitude of impact (e.g. the severity of its effect on habitat quality or

104   average population size); and (iii) covariation: whether multiple sites are impacted

105   simultaneously (i.e. the extent to which impacts are spatially correlated).

106   Demographic, genetic and environmental stochasticity are all potentially more damaging for

107   smaller populations, so increasing population sizes by increasing habitat quality ('Better')

108   and expanding existing habitat patches ('Bigger') should dampen fluctuations in population

109   size, and enhance resilience to local stochasticity and perturbations. For perturbations that are

110   less specific, more intense and/or spatially correlated, the roles of habitat creation ('More')

111   and enhancing connectivity ('Joined') are more important, by promoting metapopulation

112   dynamics or geographic range shifts. Thus, the relative importance of the BBMJ strategies

113   depends on the spatiotemporal scale of pressures that the system experiences, but the ordering

114   reflects their significance for population viability at the landscape scale (Lawton, *et al*., 2010;

115   Hodgson *et al*. 2011).

116   'Bigger' sites are likely to contain larger populations on average, which are better buffered

117   against variable conditions. The impacts of 'Better' are much the same as 'Bigger', since

118   quality can be conceptualised in terms of an increase in population carrying capacity. 'More'

119   sites improve the capacity of the network to withstand perturbations, e.g. through

120   (re)colonization and rescue effects, thus increasing the chance that some populations survive

121   a global perturbation. Finally, 'Joined' sites facilitate movement through the network, which

122   is valuable in the face of global change. In practice, BBMJ strategies should be implemented

123   jointly according to both need and opportunity.

124   **Ecological Theory to Support Resilient Ecological Networks**

125   Network resilience is hard to demonstrate since it only becomes apparent when monitored

126   over long periods. Nonetheless, theory and empirical evidence provide insights into how it

127   could be measured and enhanced.

128   Classic metapopulation theory has guided much thinking in terms of managing habitat

129   networks to improve species' persistence (Cadotte *et al.* 2017). Metapopulation structure is

130   related to all four BBMJ strategies, and the metapopulation approach has been able to predict

131   species' persistence and expansion across landscapes (Nowicki *et al.* 2007; Hooftman *et al*.

132   2016). Metapopulation capacity measures the ability of a single-species network to support a

133   viable metapopulation (Hanski & Ovaskainen 2000), and is enhanced when many large

6

134   patches are clumped in space. However, clumping can result in large gaps between

135   metapopulations, creating barriers to range expansion, so there is a trade-off (Hodgson *et al.*

136   2012).

137   Spatial network theory leads to comparable conclusions; persistence and resilience are

138   governed by both the distribution of nodes (habitat patches or populations) and the links

139   among them. Both overall connectedness and the existence of connected sub-systems

140   (modules) are important (Fortuna *et al.* 2006; Gilarranz *et al.* 2017). Approaches for

141   describing network structure include least-cost path analysis, least-cost corridors, graph

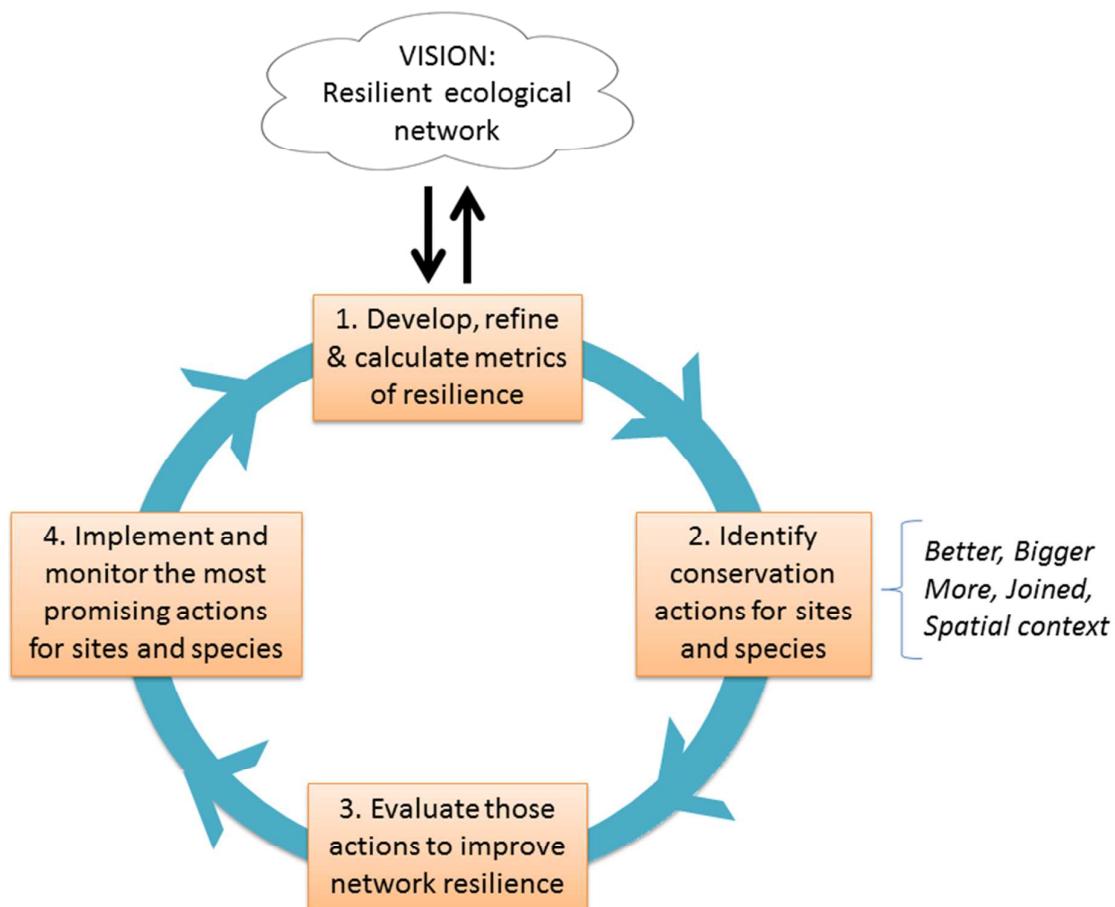142   theory and circuit theory (Laita *et al.* 2011).

143   Thus, there is a strong theoretical and empirical basis for the planning of ecological networks.

144   Different modelling frameworks reach similar conclusions despite different assumptions.

145   Spatially-realistic simulations are becoming increasingly possible (Bocedi *et al.* 2014; Gilbert

146   *et al.* 2017), and the dynamics of multiple species across real landscapes can now be

147   projected in space and time. However, such simulations are data-hungry, and faster progress

148   might be made using simpler metrics from metapopulation, graph and circuit theories. There

149   is a need to research the strengths of these approaches, so as to develop easily-obtained,

150   robust, metrics for network resilience.

151   **Resilient Ecological Networks in Practice**

152   We suggest a five-stage adaptive management framework (Westgate *et al.*, 2013) for

153   designing and delivering a resilient network (Figure 1). Each assessment of resilience (step 1)

154   would be informed by actions implemented in previous iterations (step 4) and evidence of

155   their effectiveness (step 5), as well as new knowledge, new opportunities for action and

156   changing environmental pressures. The following sections describe these steps in detail.

157

7

158   *Figure 1: Adaptive Management Cycle for implementing a resilient ecological network. The*

159   *Vision specifies the desirable network that is resilient to future pressures. Theory-based*

160   *proxies for resilience are becoming available, based on scientific tools and techniques that*

161   *are continually developing (black arrows). Features of the existing network would be*

162   *evaluated regularly to determine the likelihood that the vision will be achieved (1). Plausible*

163   *conservation actions focussed on sites or species would be identified (2) and evaluated for*

164   *their potential to improve network resilience (3). Actual conservation actions are directed at*

165   *sites or species (4), and their effectiveness monitored (5).*

166

167   ***1) Assess resilience using measurable network features***

168   Network metrics can be developed using the theory described above. For example, species-

169   specific habitat models can be used to identify the distribution of suitable patches (e.g.

8

170	Lawson *et al.* 2012), and metrics such as metapopulation capacity can then be estimated.

171	Network resilience can be framed in terms of its probability density at some point in the

172	future (e.g. the probability that 80% of species will exceed some threshold value in 100

173	years) for alternative scenarios. Models might be built using data for as many species as

174	possible, and extended to others by modelling 'virtual species' (Santini *et al.* 2016).
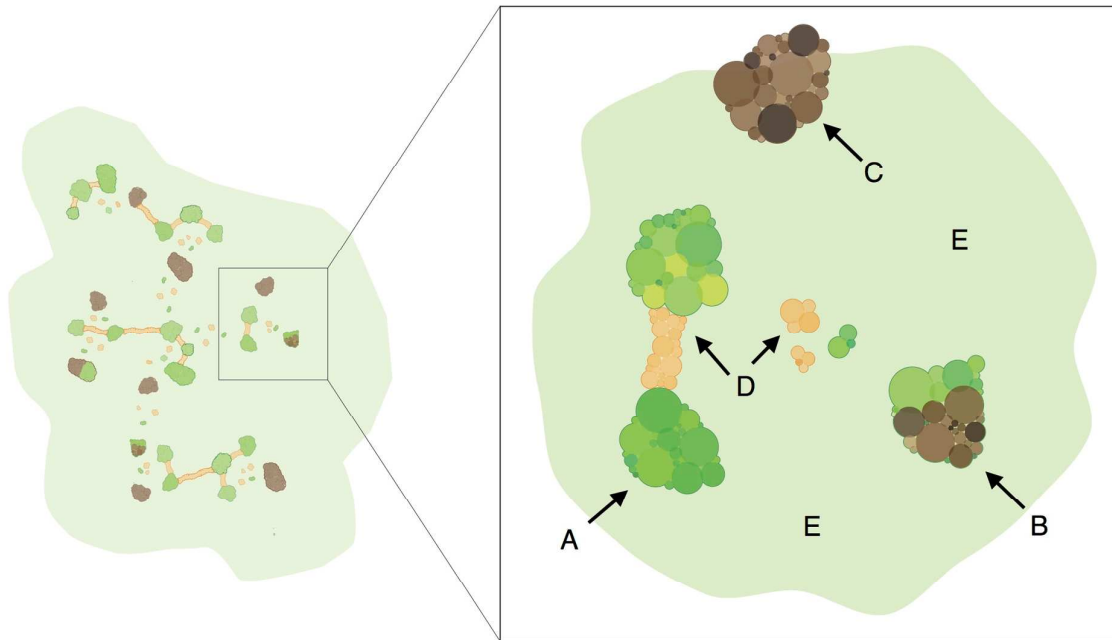
175	*2) Plausible actions to improve resilience*

176	In practice, plausible actions are limited to lower levels of organisation than the network

177	itself: sites are areas wherein conservation is practiced, and the level at which actions are

178	easiest to define (Lawton, *et al.*, 2010; Hodgson *et al.* 2011); conservation outcomes are

179	generally measured in terms of species' status.

180	Plausible actions comprise improved management (Better), expanding existing sites (Bigger),

181	and the establishment of new sites (More). These efforts can be arranged spatially (including

182	stepping-stones and corridors), and the matrix between patches 'softened' so as to increase

183	species' dispersal over multiple generations (Joined) (Figure 2). Conservation actions will

184	likely continue to target particular threatened species or communities for which the prospects

185	are poor without intervention, although successful interventions do not guarantee the

186	resilience of the network as a whole.

187

188

189 *Figure 2: An idealised ecological network. Plausible actions to increase network resilience*

190 *include improving the condition (A) or size (B) of existing sites, creating new sites (C),*

191 *creating features that facilitate dispersal (D) and softening the matrix (E).*

192

193 Many countries still have substantial areas of natural or semi-natural habitats where modest

194 actions could improve their contribution to species conservation (Sutherland *et al.* 2018).

195 However, in highly fragmented landscapes where network resilience needs to be re-built, it

196 will be necessary to create new habitat (Shwartz *et al.* 2017).

197 **3) Evaluate proposed actions in terms of potential gains in network resilience**

198 The potential effects of the plausible actions on network resilience could be evaluated in

199 terms of habitat suitability and connectivity for multiple species (Albert *et al.* 2017; Watts *et*

200 *al.* 2010). One could then use scenario-based modelling (Kukkala & Moilanen 2013) to

201 identify those locations at which action (e.g. habitat creation or improvement) may deliver

202 the biggest gain. Resilient networks also need to facilitate shifts in species' distributions.

10

203   Metrics based on circuit theory provide a convenient way to simulate the expected flow of

204   species under alternate network configurations (Hodgson *et al.* 2016).

205   ***4) Implement and Monitor***

206   The best actions identified in (3) would be enacted and their effectiveness monitored, both at

207   local sites and across the overall network. The timescales for success (increased network

208   resilience) may be long (decades) but modelling tools and continued monitoring (Box 2) will

209   feed into future iterations of the cycle (Figure 1).

210   **Delivering Network Resilience through England's 25 Year Environment Plan**

211   Our iterative approach towards enhancing network resilience will require major time and

212   resource commitments, which contrasts with the need to carry out remedial actions urgently.

213   As an interim, the principles of BBMJ and spatial network theory suggest a suite of actions,

214   which we outline for England in Box 1 that can have immediate benefits with negligible risks

215   of adverse effects (Hodgson *et al*., 2011).

216   The targets in Box 1 relate somewhat to the 25YEP commitments (DEFRA 2018), but we

217   suggest additional actions are needed to enhance the resilience of England's ecological

218   networks. The commitment to restore 75% of protected sites is similar to target (i) in Box 1,

219   and recognises the need for concerted efforts in habitat management. While the 25YEP calls

220   for a review of the functions of the National Parks and Areas of Outstanding Natural Beauty

221   for wildlife delivery, we suggest quantitative targets are required to expand the area of high

222   quality habitat within them (target ii). Furthermore, we suggest a more ambitious target of

223   doubling of the area of land under long-term protection (target iii). The 25YEP's commitment

224   to creating 500,000 ha of wildlife habitat would contribute towards network resilience, but

225   the spatial configuration of this habitat is critical in determining the impact on resilience

226   (target iv). Finally, there is a need for targeted habitat creation with a focus on enhancing the

                                                                                           11

227   connectivity of the countryside (target v). Over time, these targets should develop in response

228   to the accumulation of evidence and knowledge about progress towards achieving the vision

229   of network resilience.

230   **Prospects**

231   The BBMJ approach sets a path towards targeted, scientifically underpinned interventions.

232   The ecological principles underpinning resilient ecological networks are now well

233   established. The time is right for implementation, although many challenges will emerge in

234   application to the real-world.

235   Research is required to allow quantification of network resilience, both in terms of measuring

236   network features and mapping them onto area-based and species-based proxies. Achieving

237   resilience to different pressures, for multiple species, will likely suggest conflicting actions.

238   For example, increased connectivity is beneficial for movement between patches, but can

239   reduce resilience to local perturbations (Gilarranz *et al.* 2017) and promote the spread of

240   invasive species.

241   The UK government's commitment to creating a resilient network for nature under the

242   25YEP provides an opportunity to show global leadership in taking a science-led approach to

243   network planning. A network that delivers for species and habitats would provide important

244   ecosystem services and opportunities for people to enjoy them. For example, protecting large

245   areas of peatland would support wildlife, secure carbon storage, improve water quality and

246   enhance opportunities for recreation. Bringing the design of a resilient network for nature to

247   fruition would be a step-change in wildlife conservation, providing the means to integrate,

248   and reconcile, the competing demands for space in an increasingly crowded, and

249   environmentally compromised, world.

13

253

254 *Box 1. Potential targets for delivering Better, Bigger, More and Joined wildlife sites in*

255 *England. Achieving these targets would likely enhance network resilience, until a more*

256 *formal evaluation is done.*

257 **(i)   Improve the condition of protected areas.** Approximately 8% of England is

258 protected for nature conservation, underpinned by Sites of Special Scientific Interest[1], for

259 which the government has a target that 50% should be in "favourable condition"[2] by 2020

260 (currently 38%). We suggest an elevated target of 80% by ~2040 and that condition should be

261 redefined in terms of multispecies ecosystem properties, rather than for specific designated

262 features. **(=*Better*)**

263 **(ii)   Improve the condition of landscapes that are not currently protected for nature**

264 **conservation but have broader roles** (e.g. recreation and preserving natural beauty).

265 National Parks and Areas of Outstanding Natural Beauty cover ~24% of England. Expanding

266 the area of high quality semi-natural habitat to cover 40% of these landscapes (an increase of

267 33%) to enable these large areas to be foci for the development of resilient ecological

268 networks. **(=*Better & Bigger*)**

269 **(iii)   Increase the area of habitats under long-term protection for nature.** The

270 Convention on Biological Diversity (CBD) has a target of 17% of terrestrial and freshwater

271 habitats to be conserved by 2020. An appropriate target for England would be to at least

272 double the area being protected (currently 8%) by designation and other effective long-term

273 measures by ~2040. **(= *Bigger & More*)**

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[1] Sites of Special Scientific Interest (SSSI), National Nature Reserves, Special Protected Areas, Special Areas of Conservation, and Ramsar sites. Although the levels of protection vary across categories, with the highest afforded to the international designations, all categories are also designated as SSSIs, and it is this designation that provides the reporting framework for all protected areas.

[2] 'Favourable condition' indicates that the designated feature(s) within a site are being adequately conserved, appropriately managed, and are meeting site-specific monitoring targets, which are subject to regular review.

14

274 **(iv)** **Establish large habitat areas by creation and/or restoration.** This entails

275 extending current high-quality sites and linking them with new habitat. Taking account of

276 past losses, creating 500,000 ha of well-positioned semi-natural habitat would make a

277 significant contribution to establishing a resilient network, and take the total area of this

278 habitat in England to ~2.25 million ha - just over 17% land area (cf. CBD target). Focussing

279 this activity in large areas would maximise wildlife benefits, enable the incorporation of

280 innovative management (e.g. rewilding) and be more cost effective. A suitable target for

281 England would be to establish 25 new landscape-scale habitat creation areas (each totalling

282 >10k ha) by ~2040. **(= *Bigger & More*)**

283 **(v)** **Improve the quality and extent of habitat connectivity.** Linear landscape features

284 such as along roads, footpaths, hedgerows, rivers and coasts, simultaneously provide habitat

285 and connect sites. Their quality and permeability should be improved through management

286 and restoration, and this habitat should be mapped and its condition assessed. Such features

287 are often heavily used by the public and so improvement in quality and extent would also

288 benefit people's quality of life. **(=*Better & Joined*).**

289
290

291 | *Box 2: Recommendations for implementing scientifically-underpinned actions for resilient*

292 | *networks*

293 | 1. Devise theory-based metrics to assess the resilience of ecological networks based on the

294 | modelled viability of multiple species under plausible environmental change scenarios.

295 | Evaluate these metrics regularly at multiple scales.

296 | 2. Derive and evaluate proxy measures for the components of network resilience. Examples

297 | could include: area of high-quality habitat ('Better'), median patch size ('Bigger'), total area

298 | of suitable habitat for multiple species ('More') or network conductance ('Joined').

299 | 3. Monitor the impacts of interventions on ecological parameters. For example, habitat

300 | patches close to intervention sites should experience lower extinction rates, higher

301 | colonization rates, and smaller fluctuations in population size than sites in control regions.

302 **References**

303 Albert, C.H., Rayfield, B., Dumitru, M. & Gonzalez, A. (2017) Applying network theory to

304   prioritize multispecies habitat networks that are robust to climate and land-use change.

305   *Conservation Biology*, **31**, 1383–1396.

306 Bixler, R.P., Wald, D.M., Ogden, L.A., Leong, K.M., Johnston, E.W. & Romolini, M. (2016)

307   Network governance for large-scale natural resource conservation and the challenge of

308   capture. *Frontiers in Ecology and the Environment*, **14**, 165–171.

309 Bocedi, G., Palmer, S.C.F., Pe'er, G., Heikkinen, R.K., Matsinos, Y.G., Watts, K. & Travis,

310   J.M.J. (2014) RangeShifter: A platform for modelling spatial eco-evolutionary dynamics

311   and species' responses to environmental changes. *Methods in Ecology and Evolution*, **5**,

312   388–396.

313 Cadotte, M.W., Barlow, J., Nuñez, M.A., Pettorelli, N. & Stephens, P.A. (2017) Solving

314   environmental problems in the Anthropocene: the need to bring novel theoretical

315   advances into the applied ecology fold. *Journal of Applied Ecology*, **54**, 1–6.

316   Cumming, G.S. & Peterson, G.D. (2017) Unifying Research on Social-Ecological Resilience

317   and Collapse. *Trends in ecology & evolution*, **32**, 695–713.

318   DEFRA. (2018) A Green Future: Our 25 Year plan to improve the environment.

319   Fortuna, M.A., Gomez-Rodriguez, C. & Bascompte, J. (2006) Spatial network structure and

320   amphibian persistence in stochastic environments. *Proceedings of the Royal Society B:*

321   *Biological Sciences*, **273**, 1429–1434.

322   Gilarranz, L.J., Rayfield, B., Liñán-Cembrano, G., Bascompte, J. & Gonzalez, A. (2017)

323   Effects of network modularity on the spread of perturbation impact in experimental

324   metapopulations. *Science*, **357**, 199–201.

325   Gilbert, M.A., White, S.M., Bullock, J.M. & Gaffney, E.A. (2017) Speeding up the

326   simulation of population spread models. *Methods in Ecology and Evolution*, **8**, 501–510.

327   Hanski, I. & Ovaskainen, O. (2000) The metapopulation capacity of a fragmented landscape.

328   *Nature*, **404**, 755–758.

329   Hodgson, J. a., Moilanen, A., Wintle, B. a. & Thomas, C.D. (2011) Habitat area, quality and

330   connectivity: striking the balance for efficient conservation. *Journal of Applied Ecology*,

331   **48**, 148–152.

332   Hodgson, J.A., Thomas, C.D., Dytham, C., Travis, J.M.J. & Cornell, S.J. (2012) The speed of

333   range shifts in fragmented landscapes. ed W.M. Getz. *PloS one*, **7**, e47141.

334   Hodgson, J.A., Wallis, D.W., Krishna, R. & Cornell, S.J. (2016) How to manipulate

335   landscapes to improve the potential for range expansion. *Methods in Ecology and*

336   *Evolution*, **7**, 1558–1566.

337   Hooftman, D.A.P., Edwards, B. & Bullock, J.M. (2016) Reductions in connectivity and

338   habitat quality drive local extinctions in a plant diversity hotspot. *Ecography*, **39**, 583–

339   592.

340   Kukkala, A.S. & Moilanen, A. (2013) Core concepts of spatial prioritisation in systematic

341   conservation planning. *Biological Reviews*, **88**, 443–464.

342   Laita, A., Mönkkönen, M. & Kotiaho, J.S. (2011) Assessing the functional connectivity of

343   reserve networks in continuously varying nature under the constraints imposed by

344   reality. *Biological Conservation*, **144**, 1297–1298.

345   Lawson, C.R., Bennie, J.J., Thomas, C.D., Hodgson, J.A. & Wilson, R.J. (2012) Local and

346   landscape management of an expanding range margin under climate change. *Journal of*

347   *Applied Ecology*, no-no.

348   Lawton, J.H., Brotherton, P.N.M., Brown, V.K., Elphick, C., Fitter, A.H., Forshaw, J.,

349   Haddow, R.W., Hilborne, S., Leafe, R.N., Mace, G.M., Southgate, M.P., Sutherland,

350   W.J., Tew, T.E., Varley, J., & Wynne, G.R. (2010) Making space for nature: A review

351   of England's wildlife Sites and ecological network. *Report to Defra*, 107.

352   Logue, J.B., Mouquet, N., Peter, H. & Hillebrand, H. (2011) Empirical approaches to

353   metacommunities: a review and comparison with theory. *Trends in ecology & evolution*,

354   **26**, 482–91.

355   Morecroft, M.D., Crick, H.Q.P., Duffield, S.J. & Macgregor, N.A. (2012) Resilience to

356   climate change: translating principles into practice. *Journal of Applied Ecology*, **49**,

357   547–551.

358   Nowicki, P., Pepkowska, A., Kudlek, J., Skórka, P., Witek, M., Settele, J. & Woyciechowski,

359   M. (2007) From metapopulation theory to conservation recommendations: Lessons from

360   spatial occurrence and abundance patterns of Maculinea butterflies. *Biological*

361   *Conservation*, **140**, 119–129.

362   Oliver, T.H., Heard, M.S., Isaac, N.J.B.B., Roy, D.B., Procter, D., Eigenbrod, F., Freckleton,

363   R., Hector, A., Orme, C.D.L., Petchey, O.L., Proença, V., Raffaelli, D., Suttle, K.B.,

364   Mace, G.M., Martín-López, B., Woodcock, B.A. & Bullock, J.M. (2015) Biodiversity

365   and Resilience of Ecosystem Functions. *Trends in Ecology & Evolution*, **30**, 673–684.

366   Pellissier, L., Albouy, C., Bascompte, J., Farwig, N., Graham, C., Loreau, M., Maglianesi,

367   M.A., Melián, C.J., Pitteloud, C., Roslin, T., Rohr, R., Saavedra, S., Thuiller, W.,

368   Woodward, G., Zimmermann, N.E. & Gravel, D. (2017) Comparing species interaction

369   networks along environmental gradients. *Biological Reviews*.

370   Rose, D.C., Brotherton, P.N.M., Owens, S. & Pryke, T. (2016) Honest advocacy for nature:

371   presenting a persuasive narrative for conservation. *Biodiversity and Conservation*, 1–21.

372   Samways, M.J. & Pryke, J.S. (2016) Large-scale ecological networks do work in an

373   ecologically complex biodiversity hotspot. *Ambio*, **45**, 161–172.

374   Santini, L., Cornulier, T., Bullock, J.M., Palmer, S.C.F., White, S.M., Hodgson, J.A., Bocedi,

375   G. & Travis, J.M.J. (2016) A trait-based approach for predicting species responses to

376   environmental change from sparse data: how well might terrestrial mammals track

377   climate change? *Global Change Biology*, **22**, 2415–2424.

378   Shwartz, A., Davies, Z.G., Macgregor, N.A., Crick, H.Q.P., Clarke, D., Eigenbrod, F.,

379   Gonner, C., Hill, C.T., Knight, A.T., Metcalfe, K., Osborne, P.E., Phalan, B. & Smith,

380   R.J. (2017) Scaling up from protected areas in England: The value of establishing large

381   conservation areas. *Biological Conservation*, **212**, 279–287.

382   Sutherland, W.J., Dicks, L. V., Ockendon, N., Petrovan, S.O. & Smith, R.K. (eds). (2018)

383   *What Works in Conservation 2018*. Open Book Publishers.

384   Watts, K., Eycott, A.E., Handley, P., Ray, D., Humphrey, J.W. & Quine, C.P. (2010)

385   Targeting and evaluating biodiversity conservation action within fragmented landscapes:

20

386   an approach based on generic focal species and least-cost networks. *Landscape Ecology*,

387   **25**, 1305–1318.

388   Westgate, M.J., Likens, G.E. & Lindenmayer, D.B. (2013) Adaptive management of

389   biological systems: A review. *Biological Conservation*, **158**, 128–139.

390