

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

Journal:	<i>Journal of Applied Ecology</i>
Manuscript ID	JAPPL-2017-01254.R1
Manuscript Type:	Policy Direction
Date Submitted by the Author:	14-May-2018
Complete List of Authors:	Isaac, Nick; Centre for Ecology & Hydrology, Brotherton, Peter; Natural England, Bullock, James; Centre for Ecology and Hydrology, ; Gregory, Richard D; RSPB, Böhning-Gaese, Katrin; Biodiversitat und Klima Forschungszentrum Connor, Ben; British Ecological Society Crick, Humphrey; Natural England Freckleton, Rob; Sheffield Univeristy, Plant & Animal Science; Gill, Jennifer; University of East Anglia, Hails, Rosemary; CEH-Wallingford , Hartikainen, Minna; Royal Society of Biology Hester, Alison; The James Hutton Institute, Milner-Gulland, E; University of Oxford, Oliver, Thomas; University of Reading, Biology; Pearson, Richard; University College London Sutherland, William; University of Cambridge, Department of Zoology Thomas, Christian; University of York, Department of Biology Travis, Justin; University of Aberdeen, ; Turnbull, Lindsay; Oxford University, Department of Plant Sciences Willis, Kathy; University of Oxford, ; Royal Botanic Gardens Kew, Woodward, Guy; Imperial College London, Division of Ecology and Evolution; Mace, Georgina; University College London, Genetics, Evolution and Environment
Key-words:	Corridor, Climate change, Biodiversity conservation, Habitat management, Protected Area, Metapopulation, Resilience, Nature Recovery Network

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

3 Isaac, N.J.B.<sup>1,2</sup>, Brotherton, P.N.M.<sup>3</sup>, Bullock, J.M.<sup>1</sup>, Gregory, R.D.<sup>2,4</sup>, Boehning-Gaese, K.<sup>5</sup>,  
4 Connor, B.<sup>6</sup>, Crick, H.Q.P.<sup>3</sup>, Freckleton, R.P.<sup>7</sup>, Gill, J.<sup>8</sup>, Hails, R.S.<sup>1</sup>, Hartikainen, M.<sup>9</sup>,  
5 Hester, A.J.<sup>10</sup>, Millner-Gulland, E.J.<sup>11</sup>, Oliver, T.H.<sup>12</sup>, Pearson, R.G.<sup>2</sup>, Sutherland, W.J.<sup>13</sup>,  
6 Thomas, C.D.<sup>14</sup>, Travis, J.M.J.<sup>15</sup>, Turnbull, L.A.<sup>16</sup>, Willis, K.<sup>11,17</sup>, Woodward, G.<sup>18</sup> & Mace,  
7 G.M.<sup>2</sup>

8 <sup>1</sup>*Centre for Ecology and Hydrology, Benson Lane, Crowmarsh Gifford, Wallingford OX10*  
9 *8BB, UK*

10 <sup>2</sup>*Centre for Biodiversity and Environment Research, Department of Genetics, Evolution and*  
11 *Environment, University College London, London WC1E 6BT, UK*

12 <sup>3</sup>*Natural England, Unex House, Bourges Boulevard, Peterborough, PE1 1NG, UK*

13 <sup>4</sup>*RSPB Centre for Conservation Science, RSPB, the Lodge, Sandy, SG19 2DL, UK*

14 <sup>5</sup>*Senckenberg Biodiversity and Climate Research Centre Frankfurt, Senckenberganlage 25,*  
15 *60325 Frankfurt am Main, Germany, and Department of Biological Sciences, Goethe-*  
16 *Universität Frankfurt, Max-von-Laue-Straße 9, 60438 Frankfurt am Main, Germany*

17 <sup>6</sup>*British Ecological Society, Charles Darwin House, 12 Roger Street, London, WC1N 2JU,*  
18 *UK*

19 <sup>7</sup>*Department of Animal and Plant Sciences, University of Sheffield, Sheffield, S10 2TN, UK*

20 <sup>8</sup>*School of Biological Sciences, University of East Anglia, Norwich Research Park, Norwich,*  
21 *NR4 7TJ, UK*

22 <sup>9</sup>*Royal Society of Biology, Charles Darwin House, 12 Roger Street, London, WC1N 2JU, UK*

23 <sup>10</sup>*James Hutton Institute, Craigiebuckler, Aberdeen, AB15 8QH, UK*

24 <sup>11</sup>*Department of Zoology, Walton Street, University of Oxford, Oxford, OX2 6BW, UK*

25 <sup>12</sup>*School of Biological Sciences, University of Reading, RG6 6AH, Reading, UK*

26 <sup>13</sup>*Department of Zoology, University of Cambridge, The David Attenborough Building,  
27 Pembroke Street, Cambridge CB2 3QZ, UK*

28 <sup>14</sup>*Department of Biology, University of York, Wentworth Way, York YO10 5DD, UK*

29 <sup>15</sup>*Institute of Biological and Environmental Sciences, University of Aberdeen, Aberdeen,  
30 AB24 3FX, UK*

31 <sup>16</sup>*Department of Plant Sciences, University of Oxford, South Parks Road, Oxford, OX1 3RB,  
32 UK*

33 <sup>17</sup>*Royal Botanic Gardens Kew, London, TW9 3EA, UK*

34 <sup>18</sup>*Imperial College London, Department of Life Sciences, Silwood Park Campus, Buckhurst  
35 Road, Ascot, SL5 7PY, UK.*

## 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.

59 **Keywords:** Corridor, Climate change, Biodiversity conservation, Habitat management,  
60 Protected Area, Metapopulation, Nature Recovery Network, Resilience

## 61 **Introduction**

62 It is well understood that species exhibit inter-connected dynamics over large areas ( $>>10^3$   
63  $\text{km}^2$ ). 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.

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

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.

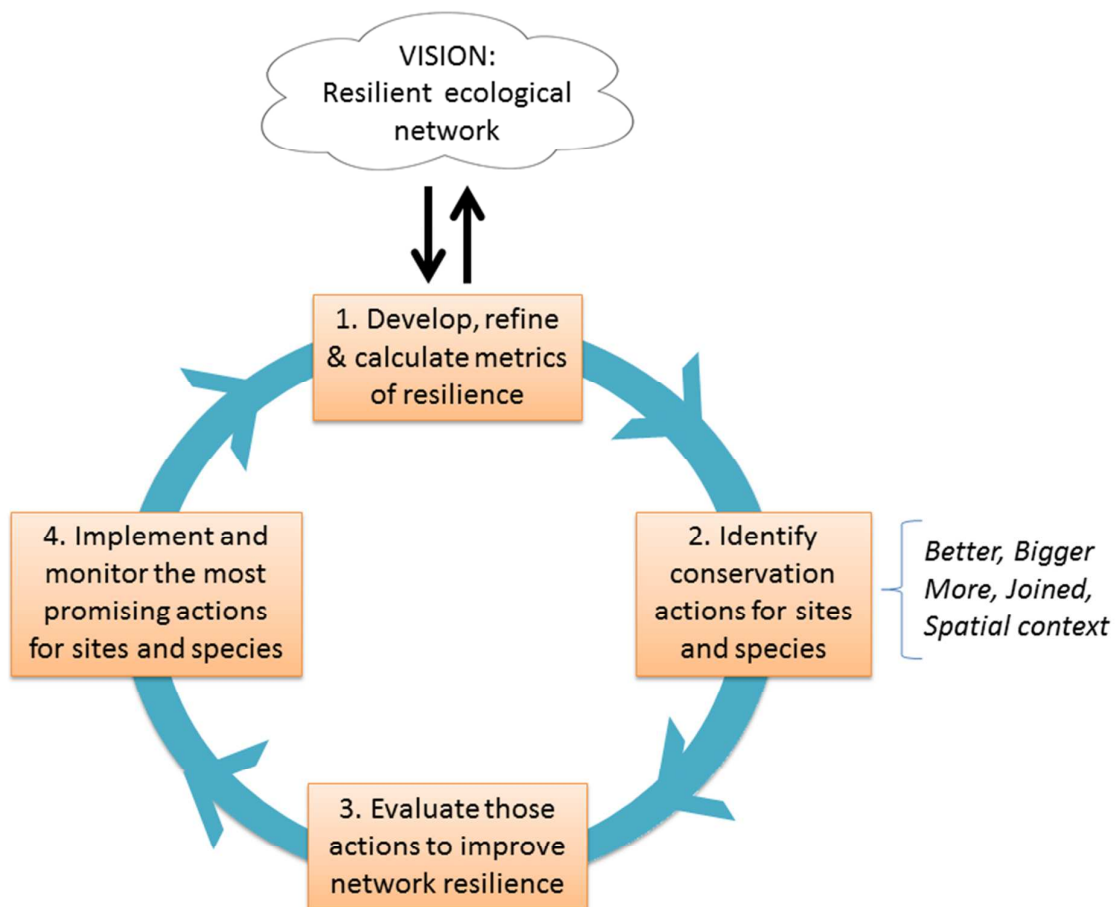
### 151 **Resilient Ecological Networks in Practice**

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



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.

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**

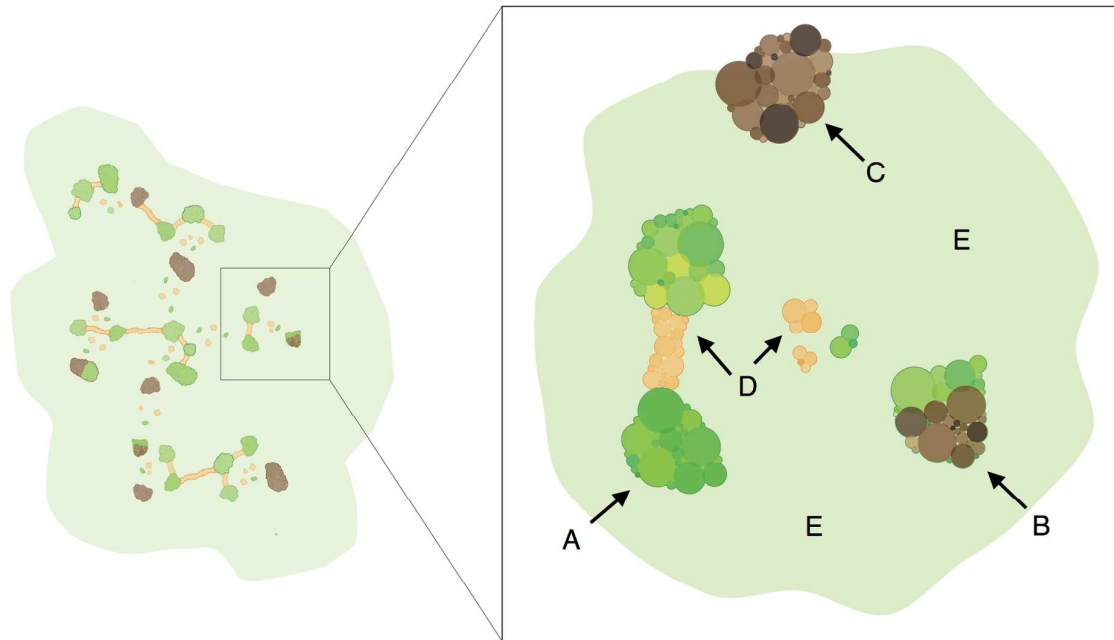
176 In practice, plausible actions are limited to lower levels of organisation than the network  
177 itself: sites are areas wherein conservation is practiced, and the level at which actions are  
178 easiest to define (Lawton, *et al.*, 2010; Hodgson *et al.* 2011); conservation outcomes are  
179 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.

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

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.

250 **Acknowledgements**

251 We thank the Natural Capital Initiative for funding, and Jenny Hodgson and two anonymous  
252 reviewers for constructive reviews.

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<sup>1</sup>, for  
259 which the government has a target that 50% should be in “favourable condition”<sup>2</sup> 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)

---

<sup>1</sup> 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.

<sup>2</sup> ‘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.

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., Pettoirelli, 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:

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