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

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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.

2. Referencing spatial network theory, we describe the conceptual basis for defining and
assessing a network of wildlife areas that supports the resilience of species to multiple
forms of perturbations and pressures. We explore actions that could enhance network
resilience at a range of scales, based on ecological principles, with reference to four
well-established strategies for intervention in a spatial network (Better, Bigger, More
and Joined) from the influential *Making Space for Nature* report by Lawton *et al.*(2010).

(2010).

Building existing theory into useable and scalable approaches applicable to large
numbers of species is challenging but tractable. We illustrate the policy context,
describe the elements of a long-term adaptive management plan and provide example
actions, metrics and targets for early implementation using England as a case study,
where there is an opportunity to include large-scale ecological planning in a newly
launched 25-year environment plan.

4. *Policy Implications*: The scientific principles to place resilience and network theory at
 the heart of large-scale and long-term environmental planning are established and
 ready to implement in practice. Delivering a resilient network to support nature
 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 $\rm km^2$). 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.

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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 demoging for

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'
- 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

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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

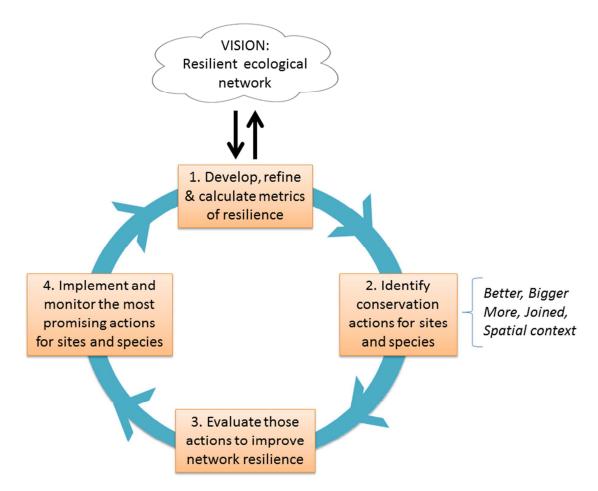
152 We suggest a five-stage adaptive management framework (Westgate et al., 2013) for

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).



167 1) Assess resilience using measurable network features

- 168 Network metrics can be developed using the theory described above. For example, species-
- specific habitat models can be used to identify the distribution of suitable patches (e.g.

Lawson *et al.* 2012), and metrics such as metapopulation capacity can then be estimated.
Network resilience can be framed in terms of its probability density at some point in the
future (e.g. the probability that 80% of species will exceed some threshold value in 100
years) for alternative scenarios. Models might be built using data for as many species as
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

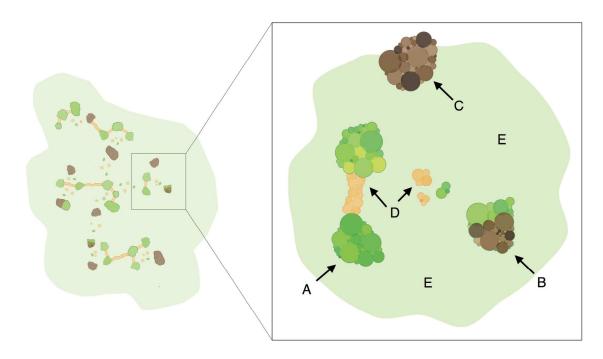
184 likely continue to target particular threatened species or communities for which the prospects

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

186 resilience of the network as a whole.

187

- 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).



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

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

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

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,

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

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

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

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

connectivity of the countryside (target v). Over time, these targets should develop in response
to the accumulation of evidence and knowledge about progress towards achieving the vision
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

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

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

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

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

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

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

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

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

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

environmentally compromised, world.

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- 252 reviewers for constructive reviews.

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 Interest¹, 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 \sim 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*)

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.

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. (= <i>Bigger & More</i>)
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	

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**

- 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
- 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

advances into the	e applied ecology	fold. Journal	of Applied Ec	ology, 54 , 1–6.
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- 316 Cumming, G.S. & Peterson, G.D. (2017) Unifying Research on Social-Ecological Resilience
- 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)
- Effects of network modularity on the spread of perturbation impact in experimental 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.
- Hanski, I. & Ovaskainen, O. (2000) The metapopulation capacity of a fragmented landscape. *Nature*, 404, 755–758.
- 329 Hodgson, J. a., Moilanen, A., Wintle, B. a. & Thomas, C.D. (2011) Habitat area, quality and
- connectivity: striking the balance for efficient conservation. *Journal of Applied Ecology*,
 48, 148–152.
- 332 Hodgson, J.A., Thomas, C.D., Dytham, C., Travis, J.M.J. & Cornell, S.J. (2012) The speed of
- range shifts in fragmented landscapes. ed W.M. Getz. *PloS one*, **7**, e47141.
- Hodgson, J.A., Wallis, D.W., Krishna, R. & Cornell, S.J. (2016) How to manipulate
- landscapes to improve the potential for range expansion. *Methods in Ecology and*
- *Evolution*, **7**, 1558–1566.
- 337 Hooftman, D.A.P., Edwards, B. & Bullock, J.M. (2016) Reductions in connectivity and

- habitat quality drive local extinctions in a plant diversity hotspot. *Ecography*, **39**, 583–
- *339 592*.
- Kukkala, A.S. & Moilanen, A. (2013) Core concepts of spatial prioritisation in systematic
 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.
- 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.
- 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.

- Logue, J.B., Mouquet, N., Peter, H. & Hillebrand, H. (2011) Empirical approaches to
- metacommunities: a review and comparison with theory. *Trends in ecology & evolution*,
 26, 482–91.
- 355 Morecroft, M.D., Crick, H.Q.P., Duffield, S.J. & Macgregor, N.A. (2012) Resilience to
- climate change: translating principles into practice. *Journal of Applied Ecology*, 49,
 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. <i>Trends in Ecology & Evolution</i> , 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. <i>Biodiversity and Conservation</i> , 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. <i>Biological Conservation</i> , 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*,
- **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.