

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

Article

Accepted Version

Isaac, N. J. B., Brotherton, P. N. M., Bullock, J. M., Gregory, R. D., Boehning-Gaese, K., Connor, B., Crick, H. Q. P., Freckleton, R. P., Gill, J. A., Hails, R. S., Hartikainen, M., Hester, A. J., Millner-Gulland, E. J., Oliver, T. H. ORCID: <https://orcid.org/0000-0002-4169-7313>, Pearson, R. G., Sutherland, W. J., Thomas, C. D., Travis, J. M. J., Turnbull, L. A., Willis, K., Woodward, G. and Mace, G. M. (2018) Defining and delivering resilient ecological networks: an example for nature conservation in England. *Journal of Applied Ecology*, 55 (6). pp. 2537-2543. ISSN 1365-2664 doi: 10.1111/1365-2664.13196 Available at <https://centaur.reading.ac.uk/77713/>

It is advisable to refer to the publisher's version if you intend to cite from the work. See [Guidance on citing](#).

To link to this article DOI: <http://dx.doi.org/10.1111/1365-2664.13196>

Publisher: British Ecological Society

including copyright law. Copyright and IPR is retained by the creators or other copyright holders. Terms and conditions for use of this material are defined in the [End User Agreement](#).

www.reading.ac.uk/centaur

CentAUR

Central Archive at the University of Reading

Reading's research outputs online

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; Biodiversität und Klima Forschungszentrum Connor, Ben; British Ecological Society Crick, Humphrey; Natural England Freckleton, Rob; Sheffield University, 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.^{1,2}, Brotherton, P.N.M.³, Bullock, J.M.¹, Gregory, R.D.^{2,4}, Boehning-Gaese, K.⁵,
4 Connor, B.⁶, Crick, H.Q.P.³, Freckleton, R.P.⁷, Gill, J.⁸, Hails, R.S.¹, Hartikainen, M.⁹,
5 Hester, A.J.¹⁰, Millner-Gulland, E.J.¹¹, Oliver, T.H.¹², Pearson, R.G.², Sutherland, W.J.¹³,
6 Thomas, C.D.¹⁴, Travis, J.M.J.¹⁵, Turnbull, L.A.¹⁶, Willis, K.^{11,17}, Woodward, G.¹⁸ & Mace,
7 G.M.²

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

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

12 ³*Natural England, Unex House, Bourges Boulevard, Peterborough, PE1 1NG, UK*

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

14 ⁵*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 ⁶*British Ecological Society, Charles Darwin House, 12 Roger Street, London, WC1N 2JU,*
18 *UK*

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

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

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

23 ¹⁰*James Hutton Institute, Craigiebuckler, Aberdeen, AB15 8QH, UK*

24 ¹¹*Department of Zoology, Walton Street, University of Oxford, Oxford, OX2 6BW, UK*

25 ¹²*School of Biological Sciences, University of Reading, RG6 6AH, Reading, UK*

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

28 ¹⁴*Department of Biology, University of York, Wentworth Way, York YO10 5DD, UK*

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

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

33 ¹⁷*Royal Botanic Gardens Kew, London, TW9 3EA, UK*

34 ¹⁸*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 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

less specific, more intense and/or spatially correlated, the roles of habitat creation ('More') and enhancing connectivity ('Joined') are more important, by promoting metapopulation dynamics or geographic range shifts. Thus, the relative importance of the BBMJ strategies depends on the spatiotemporal scale of pressures that the system experiences, but the ordering reflects their significance for population viability at the landscape scale (Lawton, *et al.*, 2010; Hodgson *et al.* 2011).

'Bigger' sites are likely to contain larger populations on average, which are better buffered against variable conditions. The impacts of 'Better' are much the same as 'Bigger', since 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 (re)colonization and rescue effects, thus increasing the chance that some populations survive a global perturbation. Finally, 'Joined' sites facilitate movement through the network, which is valuable in the face of global change. In practice, BBMJ strategies should be implemented jointly according to both need and opportunity.

Ecological Theory to Support Resilient Ecological Networks

Network resilience is hard to demonstrate since it only becomes apparent when monitored over long periods. Nonetheless, theory and empirical evidence provide insights into how it could be measured and enhanced.

Classic metapopulation theory has guided much thinking in terms of managing habitat networks to improve species' persistence (Cadotte *et al.* 2017). Metapopulation structure is related to all four BBMJ strategies, and the metapopulation approach has been able to predict species' persistence and expansion across landscapes (Nowicki *et al.* 2007; Hooftman *et al.* 2016). Metapopulation capacity measures the ability of a single-species network to support a viable metapopulation (Hanski & Ovaskainen 2000), and is enhanced when many large

patches are clumped in space. However, clumping can result in large gaps between metapopulations, creating barriers to range expansion, so there is a trade-off (Hodgson *et al.* 2012).

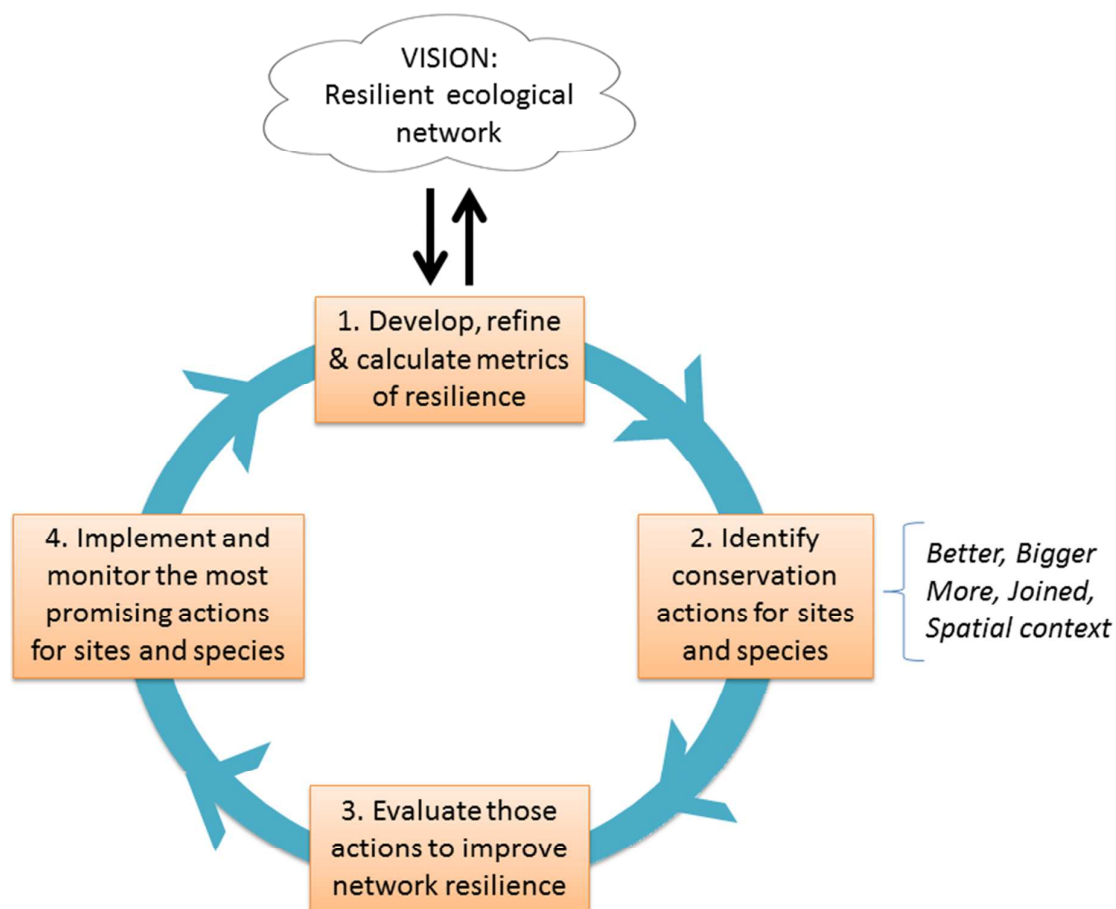
Spatial network theory leads to comparable conclusions; persistence and resilience are governed by both the distribution of nodes (habitat patches or populations) and the links among them. Both overall connectedness and the existence of connected sub-systems (modules) are important (Fortuna *et al.* 2006; Gilarranz *et al.* 2017). Approaches for describing network structure include least-cost path analysis, least-cost corridors, graph theory and circuit theory (Laita *et al.* 2011).

Thus, there is a strong theoretical and empirical basis for the planning of ecological networks. Different modelling frameworks reach similar conclusions despite different assumptions. Spatially-realistic simulations are becoming increasingly possible (Bocedi *et al.* 2014; Gilbert *et al.* 2017), and the dynamics of multiple species across real landscapes can now be projected in space and time. However, such simulations are data-hungry, and faster progress might be made using simpler metrics from metapopulation, graph and circuit theories. There is a need to research the strengths of these approaches, so as to develop easily-obtained, robust, metrics for network resilience.

Resilient Ecological Networks in Practice

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) would be informed by actions implemented in previous iterations (step 4) and evidence of their effectiveness (step 5), as well as new knowledge, new opportunities for action and changing environmental pressures. The following sections describe these steps in detail.

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.

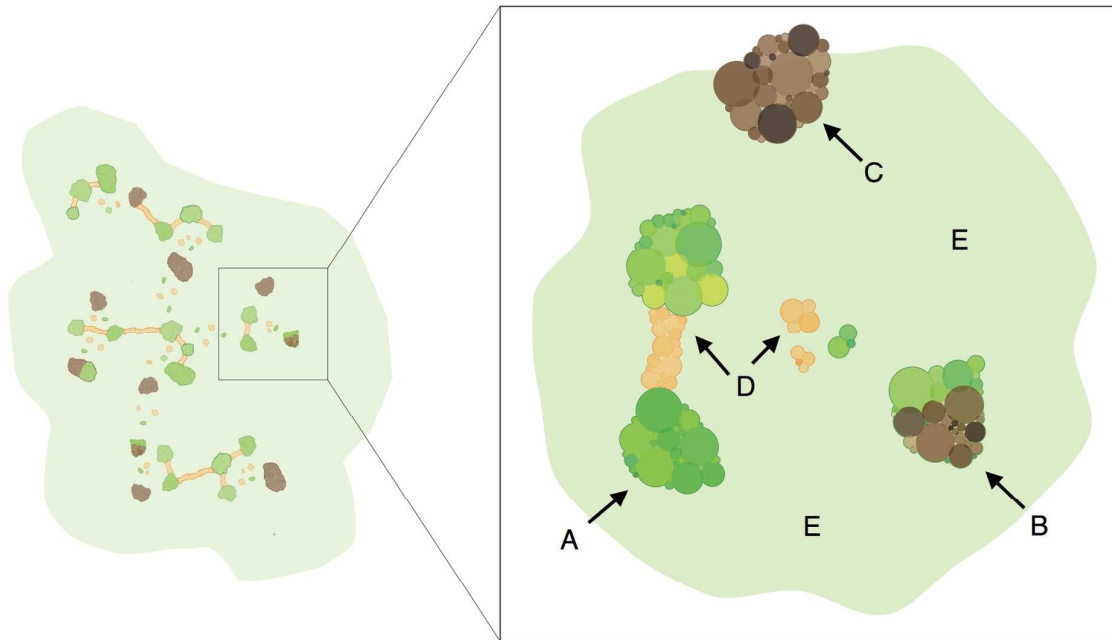
Lawson *et al.* 2012), and metrics such as metapopulation capacity can then be estimated. Network resilience can be framed in terms of its probability density at some point in the future (e.g. the probability that 80% of species will exceed some threshold value in 100 years) for alternative scenarios. Models might be built using data for as many species as possible, and extended to others by modelling ‘virtual species’ (Santini *et al.* 2016).

2) Plausible actions to improve resilience

In practice, plausible actions are limited to lower levels of organisation than the network itself: sites are areas wherein conservation is practiced, and the level at which actions are easiest to define (Lawton, *et al.*, 2010; Hodgson *et al.* 2011); conservation outcomes are generally measured in terms of species’ status.

Plausible actions comprise improved management (Better), expanding existing sites (Bigger), and the establishment of new sites (More). These efforts can be arranged spatially (including stepping-stones and corridors), and the matrix between patches ‘softened’ so as to increase species’ dispersal over multiple generations (Joined) (Figure 2). Conservation actions will likely continue to target particular threatened species or communities for which the prospects are poor without intervention, although successful interventions do not guarantee the resilience of the network as a whole.

Figure 2: An idealised ecological network. Plausible actions to increase network resilience include improving the condition (A) or size (B) of existing sites, creating new sites (C), 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). However, in highly fragmented landscapes where network resilience needs to be re-built, it will be necessary to create new habitat (Shwartz *et al.* 2017).

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

The potential effects of the plausible actions on network resilience could be evaluated in terms of habitat suitability and connectivity for multiple species (Albert *et al.* 2017; Watts *et al.* 2010). One could then use scenario-based modelling (Kukkala & Moilanen 2013) to identify those locations at which action (e.g. habitat creation or improvement) may deliver the biggest gain. Resilient networks also need to facilitate shifts in species' distributions.

Metrics based on circuit theory provide a convenient way to simulate the expected flow of species under alternate network configurations (Hodgson *et al.* 2016).

4) Implement and Monitor

The best actions identified in (3) would be enacted and their effectiveness monitored, both at 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 feed into future iterations of the cycle (Figure 1).

Delivering Network Resilience through England's 25 Year Environment Plan

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, which we outline for England in Box 1 that can have immediate benefits with negligible risks of adverse effects (Hodgson *et al.*, 2011).

The targets in Box 1 relate somewhat to the 25YEP commitments (DEFRA 2018), but we suggest additional actions are needed to enhance the resilience of England's ecological 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 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 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 (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.

Prospects

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

The ecological principles underpinning resilient ecological networks are now well established. The time is right for implementation, although many challenges will emerge in application to the real-world.

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

The UK government's commitment to creating a resilient network for nature under the 25YEP provides an opportunity to show global leadership in taking a science-led approach to 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.

250 **Acknowledgements**

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

253

Box 1. Potential targets for delivering Better, Bigger, More and Joined wildlife sites in England. Achieving these targets would likely enhance network resilience, until a more formal evaluation is done.

(i) Improve the condition of protected areas. Approximately 8% of England is protected for nature conservation, underpinned by Sites of Special Scientific Interest¹, for which the government has a target that 50% should be in “favourable condition”² by 2020 (currently 38%). We suggest an elevated target of 80% by ~2040 and that condition should be redefined in terms of multispecies ecosystem properties, rather than for specific designated features. (=Better)

(ii) Improve the condition of landscapes that are not currently protected for nature conservation but have broader roles (e.g. recreation and preserving natural beauty). National Parks and Areas of Outstanding Natural Beauty cover ~24% of England. Expanding the area of high quality semi-natural habitat to cover 40% of these landscapes (an increase of 33%) to enable these large areas to be foci for the development of resilient ecological networks. (=Better & Bigger)

(iii) Increase the area of habitats under long-term protection for nature. The Convention on Biological Diversity (CBD) has a target of 17% of terrestrial and freshwater habitats to be conserved by 2020. An appropriate target for England would be to at least double the area being protected (currently 8%) by designation and other effective long-term 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.

(iv) **Establish large habitat areas by creation and/or restoration.** This entails extending current high-quality sites and linking them with new habitat. Taking account of past losses, creating 500,000 ha of well-positioned semi-natural habitat would make a significant contribution to establishing a resilient network, and take the total area of this habitat in England to ~2.25 million ha - just over 17% land area (cf. CBD target). Focussing this activity in large areas would maximise wildlife benefits, enable the incorporation of innovative management (e.g. rewilding) and be more cost effective. A suitable target for England would be to establish 25 new landscape-scale habitat creation areas (each totalling >10k ha) by ~2040. (= *Bigger & More*)

(v) **Improve the quality and extent of habitat connectivity.** Linear landscape features such as along roads, footpaths, hedgerows, rivers and coasts, simultaneously provide habitat and connect sites. Their quality and permeability should be improved through management and restoration, and this habitat should be mapped and its condition assessed. Such features are often heavily used by the public and so improvement in quality and extent would also benefit people’s quality of life. (= *Better & Joined*).

Box 2: Recommendations for implementing scientifically-underpinned actions for resilient networks

1. Devise theory-based metrics to assess the resilience of ecological networks based on the modelled viability of multiple species under plausible environmental change scenarios. Evaluate these metrics regularly at multiple scales.
2. Derive and evaluate proxy measures for the components of network resilience. Examples could include: area of high-quality habitat ('Better'), median patch size ('Bigger'), total area of suitable habitat for multiple species ('More') or network conductance ('Joined').
3. Monitor the impacts of interventions on ecological parameters. For example, habitat patches close to intervention sites should experience lower extinction rates, higher colonization rates, and smaller fluctuations in population size than sites in control regions.

References

- Albert, C.H., Rayfield, B., Dumitru, M. & Gonzalez, A. (2017) Applying network theory to prioritize multispecies habitat networks that are robust to climate and land-use change. *Conservation Biology*, **31**, 1383–1396.
- Bixler, R.P., Wald, D.M., Ogden, L.A., Leong, K.M., Johnston, E.W. & Romolini, M. (2016) Network governance for large-scale natural resource conservation and the challenge of capture. *Frontiers in Ecology and the Environment*, **14**, 165–171.
- Bocedi, G., Palmer, S.C.F., Pe'er, G., Heikkinen, R.K., Matsinos, Y.G., Watts, K. & Travis, 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**, 388–396.
- Cadotte, M.W., Barlow, J., Nuñez, M.A., Pettorelli, N. & Stephens, P.A. (2017) Solving 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