Ecological time-lags and the journey towards conservation success

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Kevin Watts[1,2]*, Robin C. Whytock[2], Kirsty J. Park[2], Elisa Fuentes-Montemayor[2], Nicholas A.

4   **Macgregor[3], Simon Duffield[4], Philip J.K. McGowan[5]**

6   [1]Forest Research, Alice Holt Lodge, Farnham Surrey GU10 4LH, UK

kevin.watts@forestresearch.gov.uk

8   [2]Biological and Environmental Sciences, University of Stirling, Scotland FK9 4LA, UK

r.c.whytock@stir.ac.uk; k.j.park@stir.ac.uk; elisa.fuentes-montemayor@stir.ac.uk

10   [3]Durrell Institute of Conservation and Ecology (DICE), School of Anthropology and Conservation, University of Kent, Canterbury Kent CT2 7NR, UK

12   n.macgregor@kent.ac.uk

[4]Natural England, Nobel House, 17 Smith Square, London SW1P 3JR, UK

14   simon.duffield@naturalengland.org.uk

[5]School of Natural and Environmental Sciences, Newcastle University, Newcastle upon Tyne
16   NE1 7RU, UK

philip.mcgowan@newcastle.ac.uk

18

*Corresponding author

20

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28 **Abstract**

Global conservation targets to reverse biodiversity declines and halt species extinctions are

30 not being met despite decades of conservation action. However, a lack of measurable change

in biodiversity indicators towards these targets is not necessarily a sign that conservation has

32 failed; instead, temporal lags in species' responses to conservation action could be masking

our ability to observe progress towards conservation success. Here we present our

34 perspective on the influence of ecological time-lags on the assessment of conservation success

and review the principles of time-lags and their ecological drivers. We illustrate how a number

36 of conceptual species may respond to change in a theoretical landscape and evaluate how

these responses might influence our interpretation of conservation success. We then

38 investigate a time-lag in a real biodiversity indicator using empirical data and explore

alternative approaches to understand the mechanisms that drive time-lags. Our proposal for

40 setting and evaluating conservation targets is to use milestones, or interim targets linked to

specific ecological mechanisms at key points in time, to assess whether conservation actions

42 are likely to be working. Accounting for ecological time-lags in biodiversity targets and

indicators will greatly improve the way that we evaluate conservation successes.

44

Introduction

46   The state of biodiversity continues to deteriorate despite increasing conservation efforts [1]. A

mid-term assessment of the global Convention on Biological Diversity (CBD) 2020 targets

48   indicated that we are failing to halt extinctions and reverse biodiversity declines (Target 12),

despite scattered positive signs of actions being taken (e.g. increases in protected areas;

50   Target 11) [2]. Although achieving a target to show a measurable improvement in biodiversity

during the 10 years of the present CBD Strategic Plan was arguably ambitious, the lack of

52   demonstrated progress towards this and other targets on the state of biodiversity is a cause

for concern [3]. It has been suggested that poor progress towards these targets may be due to a

54   combination of increasing negative pressures on biodiversity and considerable time-lags in

species' responses to conservation actions [1]. Therefore, a lack of measurable change in

56   biodiversity indicators is not necessarily a sign that conservation actions have failed; at least in

part it could simply be that insufficient time has elapsed [4–7]. However, disentangling whether

58   success is yet to be realised or whether action has been insufficient or inappropriate is a major

challenge.

60

Ecological time-lags relate to the rebalancing of a system following a perturbation. For

62   species, populations and communities this may take the form of an 'extinction debt' following

a negative change (e.g. habitat loss, habitat degradation, invasive species, fire and climate

64   change) in which species do not disappear immediately but respond after a considerable delay

[5,7–10]. In contrast, a 'colonisation credit' (also referred to as an 'immigration' or 'species' credit

66   - see [10] for terminology) can be considered the flip-side to extinction debt, where there is a

delayed species response to conservation interventions (e.g. restoration of degraded habitat,

68   habitat creation or actions to improve connectivity between isolated fragments) [4,7,10–13].

Extinction debts and colonisation credits have been observed globally in a wide range of

70   taxonomic groups (including plants, invertebrates, vertebrates, fungi and lichens [5,7,10]) and

ecosystem types (including grasslands, temperate forests, tropical forests and urban

72   ecosystems [5,7,10]). They have also been found to operate on timescales from decades to

millennia and at local to regional spatial scales [4,7,9,10,13,14].

74

Conservation scientists increasingly acknowledge time-lags as important drivers of ecological

76   community dynamics, however, these have not been explicitly translated into conservation

policy and practice [4,5,7,9,10,15,16]. It is challenging to account for the effect of time-lags when

78   setting biodiversity targets, developing indicators and assessing the success of conservation

actions. However, it is vital that the conservation community is able to distinguish between

80   cases in which conservation policy and management interventions are on track to achieve

success but need more time for benefits to be realised, and those in which current

82   conservation actions are simply insufficient or inappropriate. This understanding of time-lags,

and the mechanisms driving them, may inform the development of 'smarter' biodiversity

84   targets, and associated indicators, that are more realistic in both their ambition and time-

frame. This is urgently needed as the CBD is soon to report on progress towards the 2020

86   targets and adopt a Post-2020 Global Biodiversity Framework [17]. More widely, process-driven

lags are starting to be recognised as important in setting achievable mitigation actions and

88   targets for other areas such as climate change policy [18].

90   To help bridge this gap between conservation science, policy and practice, we aim to: (i)

Review the principles of time-lags and their ecological drivers; (ii) Illustrate the impact of

92   habitat loss and restoration in a theoretical landscape on the responses of a number of

conceptual species; (iii) Investigate the existence of time-lags in a real biodiversity indicator

94   with empirical data; (iv) Explore approaches to extend empirical data to understand the

mechanisms driving time-lags. Finally, we discuss how various approaches can be combined to

96 more effectively understand ecological time-lags and incorporate them into the development

of effective biodiversity indicators to assist the journey towards conservation success.

98

Time-lags and their ecological drivers

100 Our perception of time-lags is commonly based on the comparison of species-area

relationships in past or stable landscapes, in which the species are assumed to be in

102 equilibrium, with species-area relationships in equivalent current or unstable landscapes [5–7,10].

For instance, if there were more species in a small remnant habitat patch post-disturbance

104 (e.g. deforestation) than would be expected in a similar sized, undisturbed fragment (in which

species are at equilibrium), then this is evidence of an extinction debt in the remnant patch.

106 This is because the smaller remnant patch has yet to lose the species that were previously

associated with the larger patch to which it once belonged [5,6] (Figure 1). Similarly, a shortfall

108 in the number of species within a large restored habitat patch, when compared to similar sized

patch from an equivalent undisturbed past landscape, would be indicative of a colonisation or

110 species credit.

112 **## Figure 1 – need to label figure with (a) & (b) ##**

114 However, these methods for quantifying time lags rely on relatively simple assumptions about

species-area relationships. A more comprehensive understanding of time lags can be gained

116 by drawing on theories of island biogeography [19] and metapopulation dynamics [20], which show

that the balance of species within disturbed (e.g. fragmented or restored) and stable systems

118 is governed by mechanisms affecting rates of extinction and colonisation [7,10]. In Figure 1, the

120 colonisation credit of the large restored patch may never be realised if the restored patch is simply too small or of insufficient quality to maintain populations, or if it is too isolated to be colonised (Figure 1).

122

124 The propensity for species to display a lag in their temporal response to change is influenced by a range of mechanisms operating at the level of individuals, populations and meta-populations [6,7,10]. At the individual level, traits such as life-span and habitat specificity can be

126 important [10,21]. For instance, short-lived species are expected to display short time-lags, declining quickly following negative disturbances and responding rapidly to positive

128 interventions [10,22]. In contrast, long-lived species are slower to respond to change and display long time-lags, because relatively few generations are affected by disturbances and

130 interventions [9,12,14,23,24]. Similarly, negative landscape changes may not have an immediate effect on species with low habitat specificity, as individuals could switch to a wide range of

132 alternative resources, while they may respond rapidly to positive changes (e.g. habitat restoration) as new areas are quickly utilised. In contrast, species with more specialist habitat

134 requirements may respond quickly to the loss and degradation of suitable habitat (with limited alternatives) and display longer time-lags in their response to conservation interventions as

136 their habitats (e.g. mature woodland) may take considerable time (e.g. centuries) to develop [9,12,14,23,24].

138

140 At the population level, a species' propensity to display time-lags is driven by a combination of vital rates, such as life-span and fecundity, and by the size and structure of the population. Species with small populations and slow life histories may suffer from an increased risk of local

142 extinction and respond quickly to negative change, whereas those with large populations and fast life histories may be able to persist for longer and respond quickly to positive change [5,6].

144

Movement of individuals at the meta-population level also influences species' susceptibility to

146 time-lags [10,25]. The movement between populations is influenced by the inherent dispersal

ability of a species, the spatial composition and configuration of the landscape, and

148 mechanisms operating at the individual and population level. In general, species which occur

in well-connected populations may be more resilient to extinctions and display longer

150 extinction debts because individual movements may rescue declining populations through

gene flow and locally extinct populations can be re-established through re-colonisation events

152 [25]. These species may also exhibit short colonisation credits as they have the ability to respond

rapidly to conservation actions, for example by quickly colonising restored habitat.

154

Theoretical example of time-lags in a changing landscape

156 We use a simple theoretical example to illustrate (i) how a range of ecological mechanisms

may influence a species' propensity to display a lag in its response to landscape change, and

158 (ii) how these lags can affect the evaluation of conservation success. The example is based on

the response of three 'conceptual' species groups ('generalist', 'specialist' and 'sensitive'),

160 which are constructed to possess contrasting combinations of ecological mechanisms, and

influence the way they may respond to habitat loss and habitat restoration in a simple

162 landscape (Box 1).

164 In this example, 'generalist' species are designed to have characteristics that make them

respond rapidly to change and display short time-lags. They have broad habitat requirements

166 and the ability to utilise a wide range of habitats (e.g. woodlands, gardens and other semi-

168 natural habitats) [10]. They are also constructed to be fairly short-lived, with relatively high fecundity and dispersal ability and to exist in large populations [10].

170 In contrast, our example of a 'specialist' species is largely or wholly dependent on one particular habitat type (e.g. mature woodland) or specific features (e.g. large trees) that

172 develop over long periods. These species are also constructed to be long-lived, with low fecundity and poor dispersal ability. Therefore, this combination of traits means that these

174 species respond slowly to change and demonstrate longer time-lags.

176 Our final group, 'sensitive' species, are designed to illustrate the mechanisms that make this group extremely sensitive to landscape change or perturbations. This group consists of

178 species living in small, isolated populations, with specialist habitat requirements coupled with low fecundity and very limited dispersal. We also illustrate the role that individual lifespan

180 may have on this sensitive group by looking at two contrasting options. Shorter-lived species in this group are expected to be especially prone to local extinction with little chance of rescue

182 or recolonisation, causing them to display severe declines over short time periods. By contrast, longer-lived species may be able to persist in small, isolated populations for long

184 periods. However, such species may still be lost in the long-term through the stochastic loss of small populations and the eventual decline and loss of meta-population dynamics. It is

186 important to highlight these 'sensitive' species since they may both (short-lived and long-lived) require urgent conservation interventions and are unlikely to benefit from more gradual

188 conservation actions (e.g. habitat restoration and creation).

190   Since biodiversity indicators commonly use composite indices based on species and/or habitat

associations (e.g. 'woodland birds') to evaluate conservation actions [26], we also illustrate how

192   a 'total species' indicator (based on the combined richness / abundance of generalist,

specialist and sensitive species) may respond to these negative disturbances and positive

194   interventions (Box 1). Our hypothetical conservation target is to restore biodiversity to the

pre-disturbance baseline. Through this theoretical example, we show that it is possible to

196   reach opposing conclusions about the success of conservation actions during five different

time intervals (T1-T5) that are on scales relevant to real world conservation policy indicators

198   and targets.

200   **## Box 1 need to add the following labels to the figure ##**

(a) Original habitat (top left)

202   **(b) Loss of habitat** (top middle)

(c) Restoration of habitat (top right)

204   (d) (top left of graph)

206   **Evidence of time-lags in a real biodiversity indicator**

The woodland bird indicator for England [27] tracks the trends of generalist and specialist

208   woodland birds over time from a baseline in 1970 (Figure 2). Indicators like this are commonly

used to evaluate progress towards biodiversity targets (e.g. Living Planet Index [28], Essential

210   Biodiversity Variables [26] & UK Biodiversity Indicators [29]). The drivers of these trends in

woodland birds are manifold [30–32], but changes in habitat availability (habitat loss or creation)

212   play an important role, and there is evidence that generalist woodland birds show rapid,

positive responses to woodland creation but specialists can take decades to re-colonise [22,33].

214   The index (set to 1 in 1970) shows that woodland specialist birds in England have declined by

46% since 1970 (Figure 2), while generalist woodland birds, many of which have adapted to

216   using gardens and woodlands in agricultural landscapes, have made a recovery of 14% after an

         initial decline [27]. During the same time-period, there were substantial efforts to plant

218   broadleaved woodland in England following substantial losses prior to the 1900s [34,35]. The

         annual rate of broadleaf woodland creation began to increase in the mid-1980s and peaked in

220   1994 (5,700 hectares created), and by 2005 the generalist woodland bird indicator had

         returned to the 1970 baseline (Figure 2). This recovery of generalist woodland birds,

222   combined with the increase in woodland creation, is suggestive of an 11-year colonisation

         credit. The continued decline of specialist woodland birds might suggest that conservation

224   actions for these species have been insufficient, inappropriate or targeted towards the wrong

         geographic areas. For example, conservation actions for migratory species might be more

226   effective along the migratory flyway or on the wintering grounds [32]. On the other hand, the

         lack of response to woodland creation by specialists could be an example of an extinction debt

228   (continuing to pay for past loss and degradation), combined with a considerable colonisation

         credit and a delayed response to current actions.

230

         ## Figure 2 ##

232

         The apparently rapid response of generalist birds to woodland creation in England and

234   contrasting slow response of specialists (Figure 2) is supported by empirical evidence from the

         WrEN project – a long-term, large-scale study of woodland creation sites in the UK [22,36]. The

236   project has data on the occurrence and abundance of woodland birds in n = 37 woodlands in

         England created between 10 and 110 years ago (median 20 years) [22]. Generalists birds are

238   widespread throughout these woodlands with 10 of the 11 indicator species detected, and six

         of 11 species in > 60 % of woodlands (Figure 3). In contrast, specialist birds are still either rare

240 (only three of 22 indicators species in > 60 % of woodlands) or absent (seven of 22 species,

Figure 3).

242

Figure 3

244

The time lag between woodland creation in England and colonisation by birds can be

246 quantified explicitly by examining the correlation between woodland age (i.e. time since

woodland creation) and bird relative abundance and species richness. We predicted richness

248 and abundance of generalist birds would show a weak positive, or no, relationship with

woodland age (after controlling for woodland size) because these species are widespread in

250 our relatively young woodlands. Results from generalised linear regression (Table 1) showed

that generalist richness was not correlated with woodland age, but there was a weak positive

252 relationship between woodland age and generalist abundance (Figures 4b and 4a). This

indicates that woodlands are rapidly colonised by generalist species after creation (as seen in

254 Figure 2), and that population densities continue to increase slightly over time, perhaps due to

an increase in available resources (e.g. tree cavities for nesting).

256

Table 1

258

For specialist birds, we predicted both species richness and abundance would increase with

260 woodland age. Results contradicted this expectation, however, and showed that although

abundance was positively (but weakly) correlated with woodland age (Figures 4a and 4c),

262 richness was not Figure 4b). We interpret this result to mean that our woodlands are on

average too young (median 20 years) to support many specialist species (further supported by

11

264 the apparent absence of several species, Figure 3) and we are not yet able to confidently

detect the accumulation of new species over time. This probably explains in part why the

266 specialist woodland bird indicator for England shows no response to woodland creation during

the past thirty years (Figure 2). Nonetheless, there is a strong correlation between bird

268 abundance and species richness in our woodlands [22], and an increase in abundance will likely

correspond with higher species richness in future. Although it could be argued that rarer

270 species become easier to detect as woodlands age (e.g. because of understory thinning),

rather than becoming more common, we suggest this is unlikely because the songs and calls of

272 several rarer, specialist species are actually highly conspicuous and thus easily detected, even

in relatively dense vegetation (e.g. Picus viridis, Phylloscopus sibilatrix).

274

Figure 4

276

Beyond empirical data

278 Empirical time-series data, as presented for the woodland bird indicator, are fundamental to

identify time-lags and understand the mechanisms driving them [7,10]. However, it can be

280 challenging to evaluate conservation success (with appropriate targets and indicators) using

only experimental or observational data since it is often unfeasible to monitor change over

282 appropriate timescales (decades or centuries). A recent review also noted that the majority of

time-lag studies have focussed on species' responses to negative disturbances rather than

284 positive changes arising from conservation interventions [10]. This subsequent paucity of data

to evaluate the performance of positive conservation actions, and develop indicators at

286 appropriate spatial and temporal scales, is particularly problematic [5,7,10,37].

288 As noted previously noted, the temporal lag in the species response to landscape change is

driven by a range of mechanisms (operating at the level of individuals, populations and meta-

290 populations) and their effects on rates of extinction and colonisation [4–7,10]. A lack of

understanding of the actual mechanisms that drive time-lags might be a reason why

292 conservation actions are often vague and do not target specific aspects of restoration, such as

quality, quantity or connectivity [6,7]. Similarly, it could also be a reason why many conservation

294 targets and indicators are overly ambitious or poorly defined.

296 Various modelling approaches are used to complement empirical data and investigate time-

lags and the mechanisms driving them [5,7,11]. For instance, a metapopulation was developed

298 for a rare butterfly where habitat patch occupancy, colonization, and extinction rates were

driven by patch connectivity, area, and habitat quality [38]. The model indicated a widespread

300 extinction debt among extant metapopulations necessitating conservation action to increase

the area and connectivity of suitable habitat [38]. Similarly, individual-based models of animal

302 dispersal and population dynamics are used to test the efficacy of alternative land

management or climate change adaptation strategies on species' persistence and range

304 shifting. One modelling study used eight conceptual species to represent different traits or

mechanisms related to life span, population density and modes of dispersal [39]. It was found

306 that increasing the size of small existing habitat patches was the best way to promote range

shifting, and that the effect of creating new stepping stone features, whilst beneficial to some

308 species, was far more variable. These studies and others reveal that species may go extinct

quickly in small patches and display a longer extinction debt in larger fragments [5].

310 Immigration, isolation and stochasticity have also been found to be important drivers of

species persistence in small communities [7,40,41].

312

Modelling studies hold considerable value to complement empirical studies and extend their

314   spatio-temporal scale. Such modelling also facilitates our ability to explore the mechanisms

driving time-lags and realistically simulate species' responses to environmental change [7,39,42,43].

316   They also have the potential to test alternative land change scenarios or compare the

effectiveness of different conservation actions *in silico* and provide a basis for the

318   development of biodiversity indicators. However, empirical data still has an important role to

help with model parameterisation and to ensure the outputs are realistic and achievable.

320

The journey towards conservation success

322   A greater integration of empirical evidence and theoretical modelling will greatly improve our

understanding of where time lags are likely to occur and the mechanisms driving them. This

324   combined knowledge will also ensure that biodiversity targets and indicators are set at

appropriate scales to assess progress towards conservation success [39,43,44]. The empirical data

326   on woodland birds collected in secondary woodlands, as part of a large-scale long-term study,

matched observations of time-lags (i.e. no lag for generalist woodland birds) observed in the

328   national bird indicator following an increase in woodland planting in England. Although this

pattern does not demonstrate causation, it is likely that the generalist bird species have been

330   able to quickly utilise newly created woodlands. The empirical data also highlighted the slow

and varied response of specialist woodland birds to woodland creation. These substantial

332   time-lags raise concerns about such species being used as biodiversity indicators, in isolation,

as they may fail to show a response for a long time and provide little evidence that

334   conservation efforts are on the right track. We recognise, however, that many specialist

species are valuable as longer-term indicators of successful conservation action (providing that

336   early successes are maintained and built on) as well as being primary conservation targets in

their own right.

338

Setting milestones, or interim targets, could be one way to ensure appropriate consideration
of time-lags and ensure that conservation policies, plans and actions are heading in the right
direction to achieve longer-term targets. Ideally, these milestones and appropriate indicators
would be informed by a combination of empirical evidence, where available, and theoretical
modelling, that make specific links to the underlying mechanisms driving species' responses to
conservation actions. This explicit link will ensure that biodiversity targets and indicators are
realistic, in both their ambition and time-frame.

346

Clearly defined temporal milestones, between primary conservation targets, should represent
key points along the path towards conservation success (e.g. Figure 5). For instance,
conservation targets and interim milestones could consist of: (Milestone 1) establishment of
policies and plans to restore habitat in degraded landscapes, identification of species near
extinction threshold which may require urgent conservation interventions (e.g. translocation,
ex-situ); (**Target 1**) an adequate area of habitat is being restored (e.g. CBD target 11: increase
area of protected land) to give the required species response, conceivably informed by
species-area relationships and empirical data; (Milestone 2) patches of the appropriate size,
quality and configuration have been established to allow target species to colonise and
establish populations in the restored patches. This process could utilise meta-population
and/or individual-based models which have been parameterised with empirical data. For
instance, woodland patch area was found to be the most important predictor of bird richness
and abundance in the WrEN study sites, suggesting that new woodlands should be 5 ha or
larger where possible [22]; (Milestone 3) generalist species with fairly high dispersal are starting
to arrive and utilise the habitat for foraging or movement, indicating that the restored habitat
is starting to develop suitable conditions; (Milestone 4) habitat conditions in restored habitats

364 are improving for more specialist species, for example showing an increase in structural

heterogeneity or formation of old growth features - reference states for this milestone might

be informed by empirical data from well-established areas; (Milestone 5) generalist species

366 are starting to further utilise the restored habitat e.g. for breeding, indicating improved

habitat quality; (Milestone 6) more specialist species, with moderate dispersal abilities, start

368 to utilise the restored habitats; and (**Target 2**) arrival and establishment of self-sustaining

populations of target specialist species (e.g. CBD target 12: reverse biodiversity declines), as

370 illustrated in Figure 5. Ongoing time-series monitoring of these interim milestones, using

appropriate indicators, will increase the realism of the ultimate conservations targets, and

372 confidence that they can be met [10]. If a milestone is missed at any point the cause should be

investigated and additional conservation interventions considered and applied as necessary

374 through an adaptive management framework. For example, a failure of the restored sites to

develop suitable habitat characteristics for specialist species (Milestone 4 in Figure 5) may

376 require additional site-level management actions.

378 **## Figure 5 ##**

380 The journey towards conservation success is challenging and long, often with considerable

delays from initial actions to ultimate outcomes. The use of well-informed conservation

382 targets, with a clearly identified sequence of milestones (as in Figure 5), could help to put in

place appropriate monitoring to confirm whether actions are working and heading in the right

384 direction. An increased understanding of the mechanisms behind time-lags provided by

empirical and theoretical studies would inform this development of appropriate biodiversity

386 targets, milestones and indicators, and help the conservation policy and practice community

to discern whether ecological time-lags are masking future conservation success or whether

16

388   current conservation actions are simply insufficient or inappropriate. There is now a timely

opportunity to incorporate consideration of time-lags in the construction of the Convention on

390   Biological Diversity Post-2020 Global Biodiversity Framework [17], which will be a major

statement of intent towards the CBD's Vision for biodiversity [45]. This offers the opportunity,

392   not only to consider realistic timescales to observes changes in the status of species at various

scales that can be measured, but to structure a framework that takes into account the

394   sequence of polices and actions that will be necessary to deliver those changes.

396   We predict that many successes are yet to be realised simply because of the lag between

conservation actions and species' responses, and there is a need to 'hold your nerve'

398   especially where there is strong evidence that conservation actions are appropriate and

robust. The existence of time-lags also suggests that there still may be time for conservation

400   interventions to rectify the problem. Previous conservation efforts have greatly reduced the

rate of decline for many species and protected many from extinction [5,12,46], and we must learn

402   from past successes and remain optimistic: conservation can and does work [47].

404   It is important that the existence of time-lags should not be used to avoid critical assessment

of current levels of conservation effort, and certainly not to justify any reduction in efforts.

406   We acknowledge that many other challenges must be overcome before global biodiversity is

adequately protected and restored. Nonetheless, accounting for ecological time-lags in

408   biodiversity targets and indicators will greatly improve the way that we evaluate progress

towards conservation success.

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Author contributions

422   K.W., K.J.P., E.F-M., and N.A.M. conceived and designed the WrEN Project. K.W., R.C.W.,

N.A.M. and P.J.K.M. designed the time-lags study. K.W., R.C.W. and S.D. collated and supplied

424   the indicator data. R.C.W. collected and analysed the bird data. K.W. and R.C.W. wrote the

manuscript. All authors discussed the results and contributed to the manuscript.

426

Competing Interest

428   The authors declare no competing interests.

430   **References**

1.   Tittensor, D. P. *et al.* A mid-term analysis of progress toward international biodiversity

432   targets. *Science (80-.).* **346**, 241–244 (2014).

2.   Secretariat of the Convention on Biological Diversity. *Global Biodiversity Outlook 4.*

434   *Secretariat of the Convention on Biological Diversity* **25**, (2014).

3.   Mace, G. M. *et al.* Aiming higher to bend the curve of biodiversity loss. *Nat. Sustain.* **1**, 448–451 (2018).

4.   Jackson, S. T. & Sax, D. F. Balancing biodiversity in a changing environment: extinction debt, immigration credit and species turnover. *Trends Ecol. Evol.* **25**, 153–160 (2010).

5.   Kuussaari, M. *et al.* Extinction debt: a challenge for biodiversity conservation. *Trends Ecol. Evol.* **24**, 564–571 (2009).

6.   Hylander, K. & Ehrlén, J. The mechanisms causing extinction debts. *Trends Ecol. Evol.* **28**, 341–346 (2013).

7.   Figueiredo, L., Krauss, J., Steffan-Dewenter, I. & Sarmento Cabral, J. Understanding extinction debts: spatio–temporal scales, mechanisms and a roadmap for future research. *Ecography (Cop.).* **42**, 1973–1990 (2019).

8.   Tilman, D., May, R. M., Lehman, C. L. & Nowak, M. A. Habitat destruction and the extinction debt. *Nature* **371**, 65–66 (1994).

9.   Krauss, J. *et al.* Habitat fragmentation causes immediate and time-delayed biodiversity loss at different trophic levels. *Ecol. Lett.* **13**, 597–605 (2010).

10.   Lira, P. K., de Souza Leite, M. & Metzger, J. P. Temporal Lag in Ecological Responses to Landscape Change: Where Are We Now? *Curr. Landsc. Ecol. Reports* **4**, 70–82 (2019).

11.   Cristofoli, S. & Mahy, G. Colonisation credit in recent wet heathland butterfly communities. *Insect Conserv. Divers.* **3**, 83–91 (2010).

12.   Kolk, J., Naaf, T. & Wulf, M. Paying the colonization credit: converging plant species richness in ancient and post-agricultural forests in NE Germany over five decades. *Biodivers. Conserv.* **26**, 735–755 (2017).

13.   Hanski, I. Extinction debt and species credit in boreal forests: modelling the

458   consequences of different approaches to biodiversity conservation. *Ann. Zool. Fennici*

37, 271–280 (2000).

460   14.   Naaf, T. & Kolk, J. Colonization credit of post-agricultural forest patches in NE Germany

remains 130-230years after reforestation. *Biol. Conserv.* **182**, 155–163 (2015).

462   15.   Essl, F. *et al.* Delayed biodiversity change: no time to waste. *Trends Ecol. Evol.* **30**, 375–

378 (2015).

464   16.   Metzger, J. P. *et al.* Time-lag in biological responses to landscape changes in a highly

dynamic Atlantic forest region. *Biol. Conserv.* **142**, 1166–1177 (2009).

466   17.   CBD. Preparations for the Post-2020 Biodiversity Framework. (2019). Available at:

https://www.cbd.int/conferences/post2020.

468   18.   Brown, C., Alexander, P., Arneth, A., Holman, I. & Rounsevell, M. Achievement of Paris

climate goals unlikely due to time lags in the land system. *Nat. Clim. Chang.* **9**, 203–208

470   (2019).

19.   MacArthur, R. H. & Wilson, E. O. *The Theory of Island Biogeography*. (Princeton

472   University Press, 1967).

20.   Hanski, I. Metapopulation dynamics. *Nature* **396**, 41–49 (1998).

474   21.   Koyanagi, T. *et al.* Grassland plant functional groups exhibit distinct time-lags in

response to historical landscape change. *Plant Ecol.* **213**, 327–338 (2012).

476   22.   Whytock, R. C. *et al.* Bird-community responses to habitat creation in a long-term,

large-scale natural experiment. *Conserv. Biol.* **32**, 345–354 (2018).

478   23.   Vellend, M. *et al.* Extiction debt of forest plants persists for more than a century

following habitat fargmentation. *Ecology* **87**, 542–548 (2006).

480   24.   Cousins, S. A. O. & Vanhoenacker, D. Detection of extinction debt depends on scale and

specialisation. *Biol. Conserv.* **144**, 782–787 (2011).

482   25.   Hanski, I. & Ovaskainen, O. Extinction debt at extinction threshold. *Conserv. Biol.* **16**,

666–673 (2002).

484   26.   Pereira, H. M. *et al.* Essential Biodiversity Variables. *Science (80-.).* **339**, 277–278

(2013).

486   27.   Defra. *Wild Bird Populations in England, 1970 to 2017*. (2018).

28.   Loh, J. *et al.* The Living Planet Index: using species population time series to track

488   trends in biodiversity. *Philos. Trans. R. Soc. B Biol. Sci.* **360**, 289–295 (2005).

29.   Defra. *UK Biodiversity Indicators 2019*. (2019).

490   30.   Fuller, R. J., Noble, D. G., Smith, K. W. & Vanhinsbergh, D. Recent declines in

populations of woodland birds in Britain: A review of possible causes. *British Birds* 116–

492   143 (2005).

31.   Bowler, D. E., Heldbjerg, H., Fox, A. D., Jong, M. & Böhning-Gaese, K. Long-term

494   declines of European insectivorous bird populations and potential causes. *Conserv. Biol.*

33, 1120–1130 (2019).

496   32.   Vickery, J. A. *et al.* The decline of Afro-Palaearctic migrants and an assessment of

potential causes. *Ibis (Lond. 1859).* **156**, 1–22 (2014).

498   33.   Savory, C. J. Colonization by woodland birds at Carrifran Wildwood: The story so far.

Scottish Birds 135–149 (2016).

500   34.   Forestry Commission. *Forestry Statistics 2018*. (2018).

35.   Quine, C. P., Bailey, S. A. & Watts, K. PRACTITIONER'S PERSPECTIVE: Sustainable forest

502   management in a time of ecosystem services frameworks: Common ground and

consequences. *J. Appl. Ecol.* **50**, 863–867 (2013).

504 36. Watts, K. *et al.* Using historical woodland creation to construct a long-term, large-scale natural experiment: the WrEN project. *Ecol. Evol.* **6**, 3012–3025 (2016).

506 37. Lira, P. K., Ewers, R. M., Banks-Leite, C., Pardini, R. & Metzger, J. P. Evaluating the legacy of landscape history: extinction debt and species credit in bird and small

508 mammal assemblages in the Brazilian Atlantic Forest. *J. Appl. Ecol.* **49**, 1325–1333 (2012).

510 38. Bulman, C. R. *et al.* MINIMUM VIABLE METAPOPULATION SIZE, EXTINCTION DEBT, AND THE CONSERVATION OF A DECLINING SPECIES. *Ecol. Appl.* **17**, 1460–1473 (2007).

512 39. Synes, N. W. *et al.* A multi-species modelling approach to examine the impact of alternative climate change adaptation strategies on range shifting ability in a

514 fragmented landscape. *Ecol. Inform.* **30**, 222–229 (2015).

40. Orrock, J. L. & Watling, J. I. Local community size mediates ecological drift and

516 competition in metacommunities. *Proc. R. Soc. B Biol. Sci.* **277**, 2185–2191 (2010).

41. Halley, J. M. & Iwasa, Y. Neutral theory as a predictor of avifaunal extinctions after

518 habitat loss. *Proc. Natl. Acad. Sci.* **108**, 2316–2321 (2011).

42. Synes, N. W. *et al.* Emerging Opportunities for Landscape Ecological Modelling. *Curr.*

520 *Landsc. Ecol. Reports* **1**, 146–167 (2016).

43. Bocedi, G. *et al.* RangeShifter: a platform for modelling spatial eco-evolutionary

522 dynamics and species' responses to environmental changes. *Methods Ecol. Evol.* **5**, 388–396 (2014).

524 44. Shriver, R. K. *et al.* Transient population dynamics impede restoration and may promote ecosystem transformation after disturbance. *Ecol. Lett.* **22**, 1357–1366 (2019).

526 45. CBD. Key Elements of the Strategic Plan 2011-2020: II. VISION. (2019). Available at:

https://www.cbd.int/sp/elements/#II.

528   46.   Hoffmann, M. *et al.* The difference conservation makes to extinction risk of the world's

ungulates. *Conserv. Biol.* **29**, 1303–1313 (2015).

530   47.   Conservationoptimism.org. *2019* Available at: https://conservationoptimism.org/.

48.   R Core Team. *R: A language and environment for statistical computing.* (R Foundation

532   for Statistical Computing, 2019).

49.   Venables, W. N. & Ripley, B. D. *Modern Applied Statistics with S (Fourth Edition).*

534   (Springer, 2002).

50.   Bartoń, K. A. MuMIn: Multi-Model Inference: R package version 1.42.1. (2018).

536   Available at: https://cran.r-project.org/package=MuMIn. (Accessed: 20th May 2019)

538   **Figure legends**

540   **Figure 1** Diagram (a) illustrates the process by which a large habitat patch (dark grey) is transformed
into a smaller patch (yellow) through fragmentation; and how a small patch (dark grey) is enlarged
(green) through habitat restoration. Figure (b) illustrates the species-area relationship for stable
542   'reference' patches (dark grey) in which species are assumed to be in equilibrium - in this case using the
past landscape patches from figure (a). The smaller fragmented patch (yellow) has more species than a
544   similar size 'reference' patch (dark grey), as species are gradually lost from this previously larger patch –
indicating an extinction debt. Similarly, the larger restored patch (green) has fewer species than a
546   stable 'reference' patch as species gradually accumulate in the restored patch through time– indicating
a colonisation credit (see [5] for more examples).

548

550   **Box 1** (a) Simplified fragmented baseline landscape with different species groups occupying the grey
habitat patches; (b) the landscape undergoes a negative disturbance event and certain habitat patches
are degraded or destroyed (yellow); (c) conservation actions are targeted at the landscape and some
552   degraded habitat patches are restored (dark green) and new habitat patches created (light green); (d)
Potential responses of three distinct species groups (generalist, specialist and sensitive) and their
554   combined total richness/abundance through time (T0-T5) in response to the landscape changes
illustrated in (a) baseline, (b) habitat loss (yellow vertical line) and (c) habitat restoration and creation
556   (green vertical line). In **T0** – All species are in equilibrium with their landscape prior to the disturbance
event; **T1** – *Generalist* species respond rapidly to the disturbance event due to their short life-span.
558   *Specialist* long-lived species respond slowly to the perturbations and display a long-time lag. Small
populations of *sensitive* species (short-lived) have been pushed beyond their threshold and go extinct
560   rapidly while the long-lived *sensitive* species display a gradual decline (flagging up the need for urgent
conservation); **T2** - The *total species* metric indicates that after a steep initial drop the degree of decline
562   in species richness/abundance has reduced as *generalist* species reach a new equilibrium due to their
short life-span, large population size and high fecundity. However, *specialist* species continue to pay
564   their extinction debt. Long-lived *sensitive* species (dashed line) display a prolonged time-lag as they are
able to persist in small, isolated populations; **T3** – Conservation actions have been implemented, but the
566   restored/created habitat is not yet suitable for any of the species. As a result, the total species indicator
is still showing a downward trend, with *generalist* species failing to respond and *specialist* species and
568   long-lived *sensitive* species continuing to pay their extinction debt; **T4** - The *total species* indicator is
now showing a positive increase, as the habitat becomes suitable for *generalist* species. These short-
570   lived *generalist* species, with high dispersal & fecundity, have now managed to colonise new patches
from their existing large populations and reach a new equilibrium. The *specialist* species also stabilise as
572   their extinction debt is paid. The long-lived *sensitive* species, in small, isolated populations, are not able
to utilise or colonise the new habitat and go extinct after a long-time lag (flagging up the need for
574   alternative conservation action); and **T5** - The *total species* indictor is now showing another increase as
the new habitat has become suitable for *specialist* species, and they slowly colonise (due to their poor
576   dispersal) and establish populations from their small, long-lived populations with low fecundity. The
benefits of the conservation actions are now being realised but the *total species* indicator is falling short
578   of the pre-disturbance target.

580   **Figure 2** The woodland bird indicators (smoothed) for England showing the change in generalist (orange
line) and specialist (blue line) woodland birds over time from a baseline of 1 in 1970[27]. The black line
582   indicates the annual rate of broadleaf woodland creation in England over the same period[34]. Annual
rates of woodland creation reach a peak in 1994 and by 2005 (a lag of 11 years) the generalist woodland
584   bird indicator returned to the 1970 baseline.

586   **Figure 3** Proportion (± 95% confidence intervals) of WrEN woodlands located in England in which each
species listed in the England woodland bird indicator was recorded during surveys in 2016 (see methods
588   in [22]).

590   **Figure 4** Standardised effect sizes from the generalised linear models (Table 1) examining the
relationships between log woodland age and woodland bird relative abundance (a) and species richness
592   (b). The back-transformed predicted relationship between relative abundance of woodland specialist
birds and log woodland age (solid line and 95 % confidence intervals) is shown in (c). Patch size was held
594   at the mean value. Data are from 37 WrEN project woodlands surveyed in central England in 2016 (see
methods in [22]).

596

    Figure 5 Schematic figure representing key steps in the journey towards conservation success, from a
598   starting point of Milestone 1 through to **Target 1** (e.g. CBD target 11: increase area of protected land),
Milestones (2 – 6) and the ultimate goal of **Target 2** (e.g. CBD target 12: reverse biodiversity declines).
600   Appropriate milestones are developed in advance based on a combination of empirical data (short-
term) and theoretical modelling (long-term).

602

Ecological time-lags and conservation success

604 **Tables**

Table 1 Results from the generalised linear models testing the relationship between woodland age and
606 woodland area, and the abundance and species richness of the two woodland bird groups (specialists
and generalists). Models were fitted using a negative binomial (nb) error structure. The predictors of
608 woodland age (years) and woodland area (ha) were both log transformed. Models were fitted using R v
3.6.1 [48] with the glm.nb() function from the MASS package [49] as appropriate. Adjusted pseudo-R-
610 squared based on the likelihood ratio test was calculated using the r.squaredLR() function in the MuMIn
package [50].
612

Variable	Estimate	Standard Error	df	P
Generalist abundance: R^2 = 0.82				
Intercept	4.04	0.06	34	< 0.001
Log woodland age (years)	0.10	0.06	34	0.10
Log woodland area (ha)	0.68	0.06	34	< 0.001
Specialist abundance: R^2 = 0.73				
Intercept	2.89	0.07	34	< 0.001
Log woodland age (years)	0.13	0.07	34	0.07
Log woodland area (ha)	0.68	0.07	34	< 0.001
Generalist richness: R^2 = 0.11				
Intercept	2.07	0.06	34	< 0.001
Log woodland age (years)	-0.01	0.06	34	0.85
Log woodland area (ha)	0.12	0.06	34	< 0.001
Specialist richness: R^2 = 0.28				
Intercept	1.72	0.08	34	< 0.001
Log woodland age (years)	0.05	0.08	34	0.52
Log woodland area (ha)	0.30	0.08	34	< 0.001