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Ecological time-lags and the journey towards conservation success

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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

Ecological time-lags and conservation success

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

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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

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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 biogeography¹⁹ and metapopulation dynamics²⁰, 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

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

122

The propensity for species to display a lag in their temporal response to change is influenced
124 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

At the population level, a species' propensity to display time-lags is driven by a combination of
140 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}.

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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
152²⁵. 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-

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natural habitats)¹⁰. They are also constructed to be fairly short-lived, with relatively high
168 fecundity and dispersal ability and to exist in large populations¹⁰.

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).

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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

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216 using gardens and woodlands in agricultural landscapes, have made a recovery of 14% after an
initial decline²⁷. 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 grounds³². 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

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240 (only three of 22 indicator 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

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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 woodlands²², 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 interventions¹⁰. 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}.

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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}.

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

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Setting milestones, or interim targets, could be one way to ensure appropriate consideration
340 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
342 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
344 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
348 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
350 policies and plans to restore habitat in degraded landscapes, identification of species near
extinction threshold which may require urgent conservation interventions (e.g. translocation,
352 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
354 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
356 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
358 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
360 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
362 is starting to develop suitable conditions; (Milestone 4) habitat conditions in restored habitats

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are improving for more specialist species, for example showing an increase in structural
364 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 conservation targets, and
372 confidence that they can be met¹⁰. 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

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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 observe 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 policies 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).

Ecological time-lags and conservation success

3. Mace, G. M. *et al.* Aiming higher to bend the curve of biodiversity loss. *Nat. Sustain.* **1**, 436 448–451 (2018).
4. Jackson, S. T. & Sax, D. F. Balancing biodiversity in a changing environment: extinction 438 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* 440 *Ecol. Evol.* **24**, 564–571 (2009).
6. Hylander, K. & Ehrlén, J. The mechanisms causing extinction debts. *Trends Ecol. Evol.* 442 **28**, 341–346 (2013).
7. Figueiredo, L., Krauss, J., Steffan-Dewenter, I. & Sarmiento Cabral, J. Understanding 444 extinction debts: spatio-temporal scales, mechanisms and a roadmap for future research. *Ecography (Cop.)*. **42**, 1973–1990 (2019).
- 446 8. Tilman, D., May, R. M., Lehman, C. L. & Nowak, M. A. Habitat destruction and the extinction debt. *Nature* **371**, 65–66 (1994).
- 448 9. Krauss, J. *et al.* Habitat fragmentation causes immediate and time-delayed biodiversity loss at different trophic levels. *Ecol. Lett.* **13**, 597–605 (2010).
- 450 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).
- 452 11. Cristofoli, S. & Mahy, G. Colonisation credit in recent wet heathland butterfly communities. *Insect Conserv. Divers.* **3**, 83–91 (2010).
- 454 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. 456 *Biodivers. Conserv.* **26**, 735–755 (2017).
13. Hanski, I. Extinction debt and species credit in boreal forests: modelling the

Ecological time-lags and conservation success

- 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., Arneith, 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.* Extinction debt of forest plants persists for more than a century
following habitat fragmentation. *Ecology* **87**, 542–548 (2006).
- 480 24. Cousins, S. A. O. & Vanhoenacker, D. Detection of extinction debt depends on scale and

Ecological time-lags and conservation success

- 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-Palaeartic 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).

Ecological time-lags and conservation success

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

Ecological time-lags and conservation success

<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
 542 into a smaller patch (yellow) through fragmentation; and how a small patch (dark grey) is enlarged
 544 (green) through habitat restoration. Figure (b) illustrates the species-area relationship for stable
 546 ‘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
 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
 stable ‘reference’ patch as species gradually accumulate in the restored patch through time– indicating
 a colonisation credit (see ⁵ for more examples).

548

Box 1 (a) Simplified fragmented baseline landscape with different species groups occupying the grey
 550 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* indicator 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
 582 line) and specialist (blue line) woodland birds over time from a baseline of 1 in 1970²⁷. The black line
 indicates the annual rate of broadleaf woodland creation in England over the same period³⁴. Annual
 584 rates of woodland creation reach a peak in 1994 and by 2005 (a lag of 11 years) the generalist woodland
 bird indicator returned to the 1970 baseline.

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

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590 **Figure 4** Standardised effect sizes from the generalised linear models (Table 1) examining the
592 relationships between log woodland age and woodland bird relative abundance (a) and species richness
594 (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
at the mean value. Data are from 37 WrEN project woodlands surveyed in central England in 2016 (see
methods in ²²).

596

598 **Figure 5** Schematic figure representing key steps in the journey towards conservation success, from a
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

604 **Tables**

606 **Table 1** Results from the generalised linear models testing the relationship between woodland age and
 607 woodland area, and the abundance and species richness of the two woodland bird groups (specialists
 608 and generalists). Models were fitted using a negative binomial (nb) error structure. The predictors of
 609 woodland age (years) and woodland area (ha) were both log transformed. Models were fitted using R v
 610 3.6.1⁴⁸ with the `glm.nb()` function from the MASS package⁴⁹ as appropriate. Adjusted pseudo-R-
 611 squared based on the likelihood ratio test was calculated using the `r.squaredLR()` function in the MuMIn
 612 package⁵⁰.

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