Received: 6 November 2025 | Accepted: 17 April 2026

DOI: 10.1111/cobi.70362

Conservation Biology

CONTRIBUTED PAPER

Optimizing biodiversity offsetting for habitat succession and colonization dynamics

Konstans Wells[1] | **Luca Börger**[1] | **Miguel Lurgi**[1] | **Kevin Watts**[2,3] | **James M. Bullock**[4]

[1]Department of Biosciences, Swansea University, Swansea, UK

[2]Biological and Environmental Sciences, University of Stirling, Stirling, UK

[3]Forest Research, Farnham, UK

[4]UK Centre for Ecology & Hydrology, Wallingford, UK

Correspondence
Konstans Wells, Department of Biosciences, Swansea University, Swansea SA2 8PP, UK. Email: k.l.wells@swansea.ac.uk

Article impact statement: Effective biodiversity offsets need ample area, long-term protection, and timelines aligned with ecological recovery and landscape context.

Funding information
Royal Society, Grant/Award Number: RGS\R2\222152; British Ecological Society, Grant/Award Number: SR23\1463; Natural Environment Research Council, Grant/Award Number: NE/V006525/1

Abstract

Biodiversity offsetting aims to compensate for ecological losses from development through conservation and restoration. However, its long-term outcomes under repeated impact–offset cycles remain uncertain. Using a conceptual forest succession model, we evaluated how offset outcomes are affected by interactions among compensation scale, duration of protection, habitat conversion rate, and land availability constraints. Additionally, we considered that these outcomes may differ across biodiversity components, including habitat maturity associated with successional habitat-forming species and metapopulation dynamics of persistent colonizers and successional specialists. We showed that effective offsetting requires restoring areas larger than those impacted and maintaining protection over timescales aligned with ecological recovery, particularly where ongoing habitat conversion reshapes landscape structure. High rates of habitat conversion consistently reduced offsetting success, particularly for colonizing species reliant on habitat quality and long-term protection. Our results further showed that delayed ecological responses and cumulative impacts can undermine offsetting efforts that appear effective in the short term. Robust offset design must therefore explicitly account for temporal lags, dynamic landscape trajectories, adequate spatial compensation, and multiple biodiversity indicators to avoid the ecological fallacy that short-term restoration success equates to long-term biodiversity and ecosystem integrity.

KEYWORDS
biodiversity offsetting, bioeconomy, biological systems dynamics, ecological compensation, habitat restoration, restoration dynamics, successional dynamics

INTRODUCTION

With ecosystem collapse considered a major socioenvironmental risk, substantial scientific and political debate has focused on how to achieve more sustainable resource use to halt and reverse biodiversity loss (Griscom et al., 2017; Leclère et al., 2020; Seddon et al., 2020). Historically, human well-being has depended on exploiting natural resources, and the resulting impacts have threatened a quarter of all species (Díaz et al., 2019; Winkler et al., 2021). Across countries, national polices include biodiversity offsetting schemes that are designed to compensate biodiversity losses from development at one location by restoring degraded ecosystems or enhancing the protection of threatened biodiversity at another location, targeting a goal of no net loss (NNL). In parallel, biodiversity credit systems certify conservation actions that generate measurable, additional biodiversity gains (Wauchope et al., 2024; Wunder et al., 2025). Together, these approaches aim to support nature-positive outcomes and advance global sustainability targets (Bull & Strange, 2018; Wauchope et al., 2024; Wunder et al., 2025; zu Ermgassen et al., 2019). However, conventional nature-based offsetting and NLL schemes are controversial because it is unclear whether compensation strategies can reliably achieve long-term sustainability goals, given the challenges of quantifying both ecological

and financial assets (Balmford et al., 2023; Bull et al., 2016; Gibbons et al., 2018; Sonter et al., 2020; Swinfield et al., 2024).

A fundamental challenge for compensatory mitigation strategies is the long timescale of ecological recovery. This is especially relevant for ecosystems where habitat-forming species, such as trees, have long generation times and where succession occurs over decades to centuries (Piovesan & Biondi, 2021). Moreover, assessments of restoration success should not focus solely on habitat-forming species, as other species and facets of biodiversity and ecosystem functioning may require longer recovery periods, assisted colonization, or specific habitat features (Dobson et al., 2025; Fagan et al., 2010; Martin et al., 2013). Thus, time delays in achieving compensation and uncertainty over whether restored ecosystems will recover are impediments to offsetting schemes that overlook long-term ecological dynamics (Buschke & Brownlie, 2020; Moilanen et al., 2009; Watts et al., 2020).

Despite widespread recognition of these challenges, it remains unclear how the temporal and spatial dimensions of offsets interplay to determine long-term biodiversity outcomes. Specifically, understanding how the size of offset areas, duration of conservation commitments, rates of habitat conversion, and species-specific dispersal and successional traits interact to influence the effectiveness of iterative development–offset cycles is critical information needed to guide policies that balance short-term development pressures with long-term conservation objectives.

Additional challenges exist when implementing offsets to achieve NNL. First, when biodiverse habitats are lost to development, like-for-like compensation must consider both the area needed to match the lost ecological value and whether sufficient land can be made available through reallocation from existing land uses (Maron et al., 2025). Second, because restoration involves ecological succession from degraded to mature states, the time required to reach target conditions must be considered. In this context, passive restoration relies on natural regeneration and is slower but less costly, whereas active restoration accelerates recovery through planting or habitat engineering (Chazdon et al., 2024).

However, debate continues over which approach is more efficient for meeting urgent conservation goals. Active restoration can shorten succession timelines, but its ability to do so is limited because trees can only be replanted as saplings, providing a fraction of the full generation period of habitat-forming species (Bauld et al., 2023; Crouzeilles et al., 2017; Kalliolevo et al., 2025). Third, if biodiversity restoration relies on colonization by species from surrounding areas, then offset areas must be connected and large enough to support dispersal and population persistence (Maron et al., 2025). Although these issues are widely recognized, their combined influence on long-term biodiversity outcomes under iterative development–offset cycles is poorly understood.

To address these challenges, we developed a spatially explicit simulation of forest restoration offsets (Figure 1). We designed the model to represent a landscape of habitat patches and lower-quality marginal patches available for restoration. Patches transition among states (protected, habitat, marginal, impacted, and offset) through successive development and offset actions (Figure 1a–c). Trees as habitat-forming species occur initially only on protected or habitat patches, and they undergo age-based successional dynamics until local conservation commitments expire. The resulting temporal mosaic of patch ages drives colonization by two generic species types: persistent colonizers, which occupy mature patches, and successional specialists, which depend on intermediate-aged forests (Figure 1d). We used scenario-based simulations to examine combinations of six policy parameters governing offsetting rules and three colonization traits (Table 1).

Our study specifically aimed to evaluate how spatial compensation, conservation duration, habitat conversion rates, and species dispersal traits interact to determine the success of biodiversity offsets. We further assessed how temporal lags in ecological recovery and landscape-scale processes affect habitat quality, ecosystem structure, and metapopulation persistence over long timeframes.

Our results showed that achieving NNL over time requires offsets that exceed the area of impacted areas and the implementation of long-term conservation commitments. Offsetting frameworks must explicitly incorporate robust biodiversity indicators, landscape context, and ecological time lags to ensure that compensation genuinely maintains or enhances biodiversity. Importantly, the simulation framework presented here is readily adaptable to other ecosystems, such as grasslands, where recovery dynamics operate over different temporal scales.

MATERIALS AND METHODS

We implemented a conceptual, spatially explicit modeling framework (Figure 1) to explore alternative biodiversity offsetting scenarios involving forest restoration. The framework follows recommended standards for ecological simulations (Planque et al., 2022). To ensure ecological interpretability, we parameterized processes and time scales around forest succession, for which empirical data on tree growth and stand dynamics are widely available.

The model quantified long-term biodiversity outcomes of alternative compensation strategies for development-driven habitat loss. It explicitly integrated forest succession through age-structured dynamics of habitat-forming trees and evaluated offset effectiveness for two types of colonizer species with contrasting life-history traits (persistent vs. early successional colonizers) that represent species that are not translocated but rely on natural colonization of restored areas (Bauld et al., 2023).

The model design was based on a virtual landscape comprised of M patches randomly distributed in two-dimensional space. Patches were characterized by a set of state variables that included (1) patch type (protected, habitat, marginal, impacted, and offset; definitions and associated processes described below) and (2) occupancy state (presence and absence) of each colonizer species subject to spatial metapopulation dynamics. The model also included individual trees, which were allocated to certain patches and characterized by age as a state variable. For all patches with trees, the patch- and time-specific mean tree age was summarized as the state variable patch quality. Specifically, we assumed that the average stand age of a forest was a

TABLE 1 Description and values of all sampled, fixed, and monitored parameters used in the conceptual modeling framework (justifications for parameter choices are provided in Appendices S2 & S3).

Parameters	Symbol	Description	Value
Sampled parameters			
Proportion of protected patches	pProtect	Proportion of protected patches in the model landscape	Range of 0.01–0.2 (increments of 0.02)
Number of impacted patches	$N_{impacted}$	Number of patches to be impacted per time step	Range of 2–10 (increments of 1)
Habitat impact ratio	hir	Proportion of impacted patches on habitat patches (and not on marginal patches)	Range of 0.1 and 1 (increments of 0.1)
Habitat compensation factor	hcf	Amount of marginal patches converted into offset patches as compensation for any impacted patch converting habitat	Range of 0.5–6 (increments of 0.5)
Conservation commitment period	ccp	Time period over which offset patches are not disturbed (during which forests mature with each time step until they reach the maximum age)	Range of 5–200 (in increments of 5 years)
Impact period	ip	Time span during which impacted patches remain affected	Range of 25–500 (in increments of 25 years)
Clustering strength	α	Spatial clustering parameter controlling the degree to which development events are spatially aggregated	Range of 0–1 (in increments of 0.1)
Habitat age threshold	$minage_{hab}$	Minimum stand age required for a patch to be suitable for colonizer species	Range of 1–50 (in increments of 5 years)
Species extinction rate	occ_{ext}	Rate that determines whether a metapopulation species may go extinct from any occupied patch (i.e., changing the occupancy state from present to absent)	Range of 0.1–0.7 (in increments of 0.1)
Maximum dispersal distance	$disp_{max}$	Maximum distance for which any suitable and empty patch will be occupied by a metapopulation species if any patch in a distance $\leq disp_{max}$ is occupied and enables colonization	Range of 5–100 m (in increments of 5 m)
Intrinsic rate of yield enhancement	r_{yield}	Intrinsic rate of yield enhancement per unit area for marginal patches in simulations exploring different yield growth models for enabling land-sparing	Range of 0.05–1.85 (10 values logarithmically spaced between min and max values)
Maximum yield intensification factor	K_{yield}	Asymptotic maximum yield intensification factor achievable by the terminal time T in simulations exploring different yield growth models for enabling land availability	Range of 1–5 (10 values logarithmically spaced between min and max values)
Fixed parameters			
Patch number		Number of patches in the simulated landscape	1000
Proportion of habitat patches		Proportion of habitat patches in the landscape	0.2
Proportion of marginal patches		Proportion of marginal patches in the landscape	$1 - (0.2 + \text{pProtect})$
Evaluation indicator			
Patch quality		Patch- and time-specific mean tree age (as a proxy for patch quality)	
Landscape quality	LQ	Ratio of the mean patch quality at any given time step to the mean initial patch quality across all patches in the landscape at the onset of the respective simulation scenario	
Habitat quality	HQ	Average patch quality divided by the average initial patch quality for patches other than protected area (a proxy for habitat loss/gain through impact–offset actions)	
Mature patch ratio	MP	Ratio of patches with trees with average tree age $\geq$50 years in the landscape relative to the total number of mature patches at the onset of simulations	
Occupancy ratio	OC	Number of patches occupied at a certain time step by a metapopulation of species divided by the number of initially occupied patches	
NNL quality		Binary indicator equal to 1 if the landscape quality ratio remained $\geq$1 at all time steps, indicating achievement of no net loss in landscape quality	

(Continues)

TABLE 1 (Continued)

Parameters	Symbol	Description	Value
95% habitat quality		Binary indicator equal to 1 if the habitat quality ratio remained ≥0.95 at all time steps, indicating limited habitat loss through impact-offsetting actions	
95% mature patches		Binary indicator equal to 1 if the mature patch ratio remained ≥0.95 at all time steps, indicating limited loss of mature patches under repeated impact-offsetting actions	
Mature patch recovery		Binary indicator equal to 1 if the ratio of mature patches remained ≥0.5 at all time steps and reached ≥1 at the final time step, indicating sustained and full recovery of mature habitat through impact-offsetting actions	
95% metapopulation persistence		Binary indicator equal to 1 if the ratio of occupied patches ≥0.95 at all time steps for persistent colonizers and successional specialists, indicating limited fluctuation in the overall patch occupancy of colonizer species	

reasonable proxy for habitat quality because this approach is supported by empirical analyses of forest restoration (Martin et al., 2013). At the start of the simulations, patches were classified into three types. Protected patches contained 100 trees, each 200 years old, representing mature forest habitat corresponding to two to three generations of habitat-forming tree species in European forests (Pretzsch, 2009). Protected patches were not available for conversion by development. Habitat patches contained 100 trees, each 50 years old, represented managed forests at an intermediate successional stage (approximately one generation time of trees), and were available for potential development. Patches classified as marginal represented other vegetation types without trees that could be allocated to development or restoration, subject to landscape dynamics and land availability constraints that are described below. We generated the proportion of protected patches in the model landscape randomly according to the parameter pProtect, whereas the proportion of habitat patches was set to 20%. All remaining patches were initially characterized as marginal.

For the colonizer species, the suitability of any patch was determined by the habitat age threshold ($\text{minage}_{\text{hab}}$) parameter given as the minimum stand age that allows a species to colonize a patch. We modeled two types of colonizer species to distinguish those capable of persisting in mature forest patches from those that cannot persist in old-growth patches. Specifically, we defined persistent colonizers as those that can colonize any forest (habitat and protected) patch ≥ $\text{minage}_{\text{hab}}$ with no upper age limit and successional specialist as those that can colonize any forest patch ≥ $\text{minage}_{\text{hab}}$ but ≤100 years of age (unable to colonize protected forest and mature offset forests >100 years old). The initial occupancy states were set to present for all habitat and protected patches.

Model processes

The model simulations involved multiple steps. First, the number of impacted patches in each time step (N_{impacted}) was randomly selected; all trees were removed from these selected habitat or marginal patches; and their state was changed to impacted. The parameter habitat impact ratio (hir) determined the proportion of N_{impacted} that affected habitat patches, with the remainder affecting marginal patches. Distinguishing these two parameters allowed the model to separate overall development intensity (N_{impacted}) from the specific impacts on habitat versus marginal land (or hir), reflecting real-world differences in expansion pressure and spatial planning or avoidance strategies. To represent spatial clustering in human development (i.e., an increased likelihood of impacts occurring near previously developed locations), we implemented a spatially explicit impact allocation procedure. Eligible patches were sampled with probabilities that decreased exponentially with distance to the nearest previously impacted patch such that the selection weight for any patch i was proportional to $\exp^{-\alpha d_i}$, where d_i is the distance to the nearest impacted patch and the sampled parameter $0 \leq \alpha \leq 1$ controls clustering strength. When $\alpha = 0$, all patches had equal selection probability (i.e., spatially random impacts), whereas increasing values of α generated increasingly clustered development patterns.

Second, for each impacted habitat patch (as determined by N_{impacted} in each time step), the habitat compensation factor (hcf) determined how many marginal patches would be converted into offset patches per impacted patch. When this product exceeded the number of available marginal patches, the selection was constrained to the available patches. Third, for offset patches, the conservation commitment period (ccp) defined how long the patches would be protected from activities that could compromise ecological integrity or forest succession. When time since restoration exceeded ccp, the state of the compensated patched was changed to habitat patch, returning it to the pool of development-eligible habitat patches. Fourth, for impacted patches, the impact period (ip) determined the time span for how long patches would be impacted. If the time span after the onset of impact exceeded the ip, then the state of impacted patches was changed to marginal. Tree age of all trees on established patches increased in each model time step by 5 years until they reached the maximum age. Finally, in the baseline model, marginal patches were available for offsetting

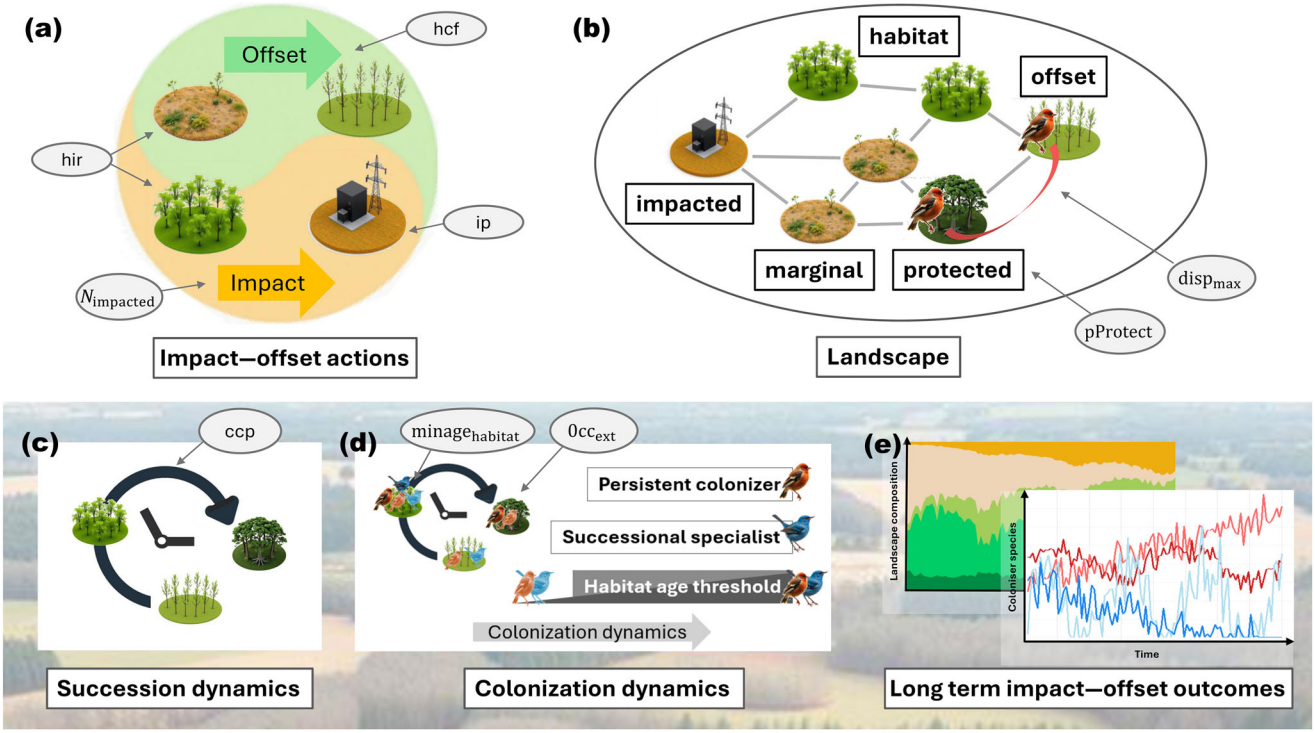

FIGURE 1 Conceptual framework of iterative impact–offset dynamics and biodiversity outcomes. Offset sites are established to compensate for habitat conversion through impact–offset actions (a), such as planting habitat-forming (tree) species. These actions change the landscape (b), which includes impacted patches, marginal patches available for offsetting, and protected patches. Habitat-forming species undergo succession over time (c), influencing colonizer species persistence (e.g., birds) according to their dispersal ability and habitat age thresholds (d). Repeated impact–offset cycles drive temporal changes in biodiversity indicators (e), illustrated schematically as long-term model outputs of stacked landscape composition (upper plot; proportions of habitat states through time) and example time series of colonizer species (lower plot; relative changes in occupancy). Scenario simulations vary key parameters governing development and restoration: habitat impact ratio (hir; proportion of impacted patches drawn from habitat vs. marginal land), habitat compensation factor (hcf; number of offset patches created per impacted patch), conservation commitment period (ccp; duration offset patches are protected before reverting to habitat), impact period (ip; duration impacted patches remain in an impacted state), maximum dispersal distance ($disp_{max}$), species extinction rate (occ_{ext}), habitat age threshold ($minage_{hab}$), proportion of protected patches (pProtect), number of impacted patches per time step ($N_{impacted}$), maximum yield intensification factor (K_{yield}), and rate of yield improvement (r_{yield}).

subject only to landscape composition and the development–offset process cycle. However, in actual landscapes, marginal land typically represents areas that are spared from production rather than unused land. We therefore extended the model to include land availability constraints that coupled offset availability to production dynamics. Yield improvements were modeled using a logistic function characterized by the maximum yield intensification factor (K_{yield}) and the rate of yield improvement (r_{yield}). At each time step, the resulting yield multiplier determined the fraction of marginal land that remained in production to maintain overall output, thereby limiting the number of patches available for restoration. When $K_{yield} = 1$, yield remained constant, and no land sparing occurred, corresponding to the baseline scenario without production-driven release of marginal land. Increasing K_{yield} allowed progressively more marginal land to be allocated to offsets, whereas r_{yield} controlled the pace at which yield gains (and thus potential land sparing) occurred through time. All calculation details are provided in Appendix S1.

In addition to the processes governing the habitat-forming species (i.e., trees), the patch occupancy dynamics of habitat-dependent colonizer species were determined by three mechanisms: patch suitability, defined by the habitat age threshold ($minage_{hab}$), representing the minimum stand age required for colonization; stochastic local extinction, governed by the species extinction rate (occ_{ext}), which determined the probability that an occupied patch becomes unoccupied; and dispersal limitation, defined by the maximum dispersal distance ($disp_{max}$), whereby any empty but suitable patch becomes colonized if at least one occupied patch occurs within a distance $\leq disp_{max}$. We quantified metapopulation abundance at the landscape scale as the number of patches occupied by the metapopulation species (N_{Occ}).

We initialized the model with $M = 1000$ patches randomly selected from a 100 × 100 cell grid. Offsetting scenarios were simulated by iteratively sampling random combinations of parameter values. Parameter ranges reflected a combination of plausible ecological values (e.g., forest age thresholds and extinction probabilities) defined jointly by the author team and normative or policy-driven choices (e.g., compensation ratios and ccps), for which empirical distributions were unavailable. For the normative or policy-driven choices, ranges were chosen

to span current practice and plausible future policy ambitions rather than to represent observed frequencies (see Appendices S2 & S3 for justifications of parameter choices). Model parameters included those governing development and compensation schemes (pProtect, $N_{impacted}$, hir, α, hcf, ccp, ip, K_{yield}, and r_{yield}) and species colonization dynamics ($minage_{hab}$, occ_{ext}, and $disp_{max}$) (Table 1).

Emerging patterns

The emerging patterns of interest were derived from simulations examining the temporal dynamics and variability in biodiversity indicators under alternative compensation scheme parameterizations. To assess patterns, we calculated landscape quality (LQ) as the ratio of the mean patch quality step to the mean initial patch quality at the onset of the respective simulation scenario across all patches in the landscape. We further calculated habitat quality (HQ) as the average patch quality divided by the average initial patch quality for patches other than protected areas (a measure accounting for the loss/gain of habitat only). Moreover, we calculated the mature patch ratio (MP) as the ratio of patches with trees with average tree age of ≥50 years in the landscape relative to the total number of mature patches at the onset of the simulations.

For the colonizer species, we calculated the occupancy ratio (OC) as the number of patches occupied at a certain time step divided by the number of initially occupied patches. We calculated these measures (LQ, HQ, MP, and OC) at time steps of 1, 2, 5, 10, 25, 50,75, 100, and 500 years after the onset of the simulations. For all scenarios, we further extracted the time step of the simulations at which marginal land was no longer available.

Model evaluation

To evaluate the model and assess whether offset targets were met, we defined eight binary evaluation indicators based on ecological state variables and assessed each against predefined threshold criteria to classify whether offset targets were achieved. These offset targets were the following: NNL quality, landscape quality ratio ≥1; 95% habitat quality, habitat quality ratio ≥0.95; 95% mature patches, mature patch ratio at all times ≥0.95; mature patch recovery, ratio of mature patches remained ≥0.5 throughout the simulation and reached ≥1 at the final time step; 95% metapopulation persistence, ratio of occupied patches ≥0.95 for persistent colonizers and successional specialists; and metapopulation recovery, ratio of occupied patches remained ≥0.5 throughout the simulation and reached ≥1 at the final time step for persistent colonizers and successional specialists. Using the offset targets classifiers, we explored the minimum values and combinations of key parameters that would achieve the targets.

For global sensitivity analysis, we used gradient boosting regression (using the gbm() function in R) to quantify the percentage of output variance explained by the sampled input parameters (pProtect, $N_{impacted}$, hir, α, hcf, ccp, ip, K_{yield}, r_{yield}, $minage_{hab}$, occ_{ext}, and $disp_{max}$). Because global sensitivity results depend on the parameter space explored, estimates of parameter importance should be interpreted as conditional on the parameter ranges rather than as intrinsic measures of ecological importance.

Because realized habitat loss was determined by the number of impacted patches and the proportion of impacts occurring on patches classified as habitat rather than marginal, we defined the habitat conversion rate (convr) as $convr = N_{impacted} \times hir/M$. This derived metric represented the effective habitat conversion rate per time step, enabling comparison across scenarios with different impact parameter combinations. For subsequent analyses, convr was categorized into three equally sized groups (low: 0.0002–0.0048, medium: 0.0048–0.0095, and high: 0.0096–0.0200) based on tertiles of its empirical distribution, allowing assessment of offset target achievement across gradients of conversion intensity.

We conducted all analyses for 100,000 scenarios of randomly selected parameter combinations. Subsampling analyses indicated that results were robust to sample size effects. All modeling and data analyses were conducted in R version 4.3.1 (R Core Team, 2024).

RESULTS

Offset scale and conservation duration shape habitat succession

Across the modeled scenarios, the NNL quality target (NLL in landscape quality) was met in ≤4% of scenarios, and the target was met only when the habitat impact ratio (hir; the fraction of development incidents affecting habitat rather than marginal patches) was ≤0.7, highlighting that low-impact development was essential for effective offsetting. The likelihood of achieving the NNL quality target was most strongly influenced by $N_{impacted}$ (the number of patches impacted per development incidence), which explained 55% of the variance in the gradient boosting analysis.

The less stringent 95% habitat quality target was achieved in 56% of the scenarios. In scenarios where development affected only habitat patches (hir = 1), a minimum hcf of 1 was sufficient to meet the target when the ccp was ≥45 years. Sensitivity analysis indicated that this target was primarily influenced by hcf (explaining 35% of variance) and $N_{impacted}$ (20% of variance) across the explored parameter ranges (see Appendix S4 for partial dependence plots).

As the simulated impact–offset actions were based on replacing habitats with restoration sites with younger trees, the fraction of mature patches inevitably decreased during the first years of impact in all scenarios (Figure 2). The 95% mature patches target was met in 12% of the simulations, and the mature patch recovery target was met in 47% of the simulations. For both mature patch targets, a minimum conservation commitment period of ccp ≥45 years (corresponding to the

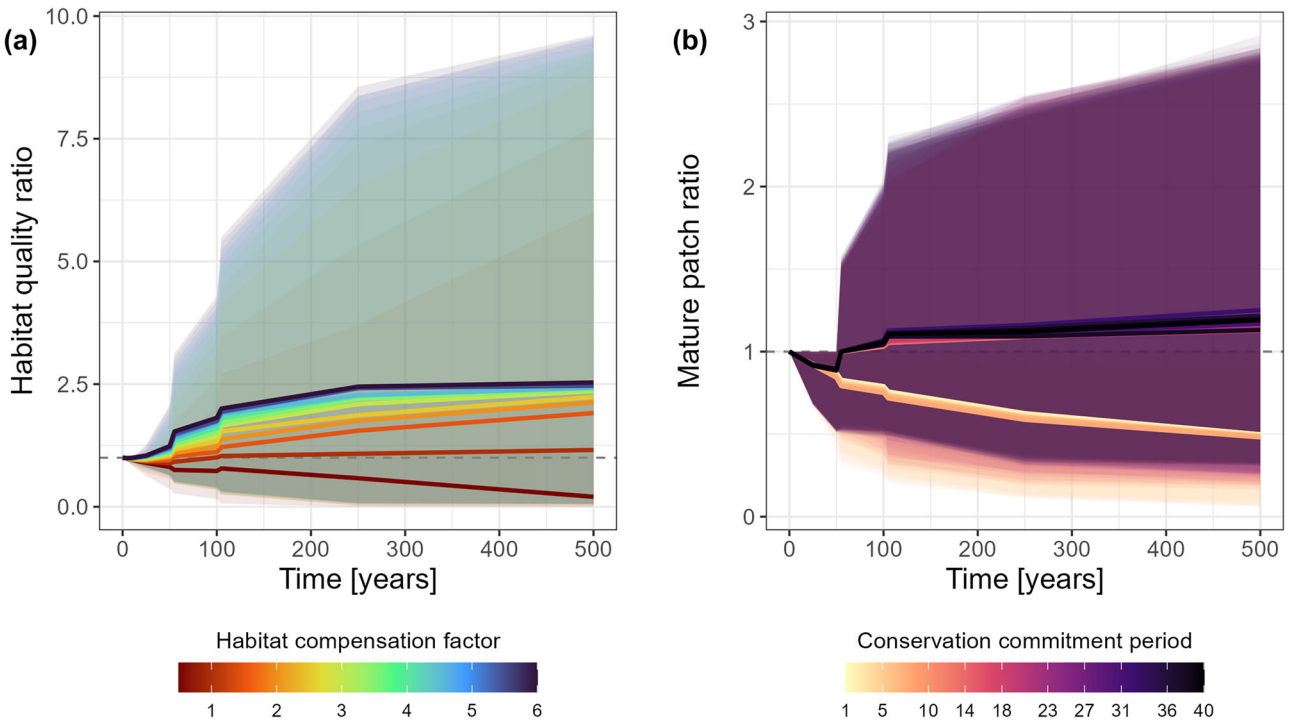

FIGURE 2 Habitat compensation factor and conservation commitment period drive the outcomes in biodiversity offsetting scenarios. Changes in landscape-scale habitat quality ratio over time (habitat quality at different times in relation to initial value) binned and color-coded for different habitat conservation factors (a) and changes in mature patch ratio over time binned and color-coded for different conservation commitment periods (b). Lines represent the median from all scenarios from the respective binning group, and ribbons represent the 95% of these binned scenarios.

age difference between impacted habitat and newly established offset sites) was the threshold for achieving the target in any scenario of full impact on habitats (hir = 1).

Achieving the 95% mature patches target was most sensitive to the habitat impact ratio (hir, 39% of the variance explained; see Appendix S5 for partial dependence plots) and to the number of impacted patches ($N_{impacted}$, 38% variance explained). The mature patch recovery target conversely was most sensitive to changes in the ccp (25% variance explained; see Appendix S6 for partial dependence plots) and the hcf (24% variance explained).

From a short-term versus long-term perspective, 39% of the scenarios that initially met the 95% habitat quality target and 82% of scenarios that initially met the 95% mature patches target during the first 10 years failed to sustain these targets over the full simulation period.

Across scenarios, marginal patches were never fully exhausted by development–offset dynamics alone; however, under land availability constraints, marginal land availability became unsustainable in 45% of simulations due to production requirements rather than biodiversity outcomes. The proportion of scenarios in which marginal land was exhausted under production constraints declined with increasing maximum yield intensification factor (K_{yield}), from 79% at $K_{yield} = 1$ to approximately 30% at $K_{yield} \geq 4$ (Appendix S7).

Synergistic effects of habitat conversion and species traits on colonizer persistence

The 95% metapopulation persistence target was met more often for persistent colonizers than for successional specialists (38% and 16% of simulation scenarios, respectively). Persistent colonizers and successional specialists with habitat age thresholds of $minage_{hab} \leq 30$ years met this target in 79% and 85% of scenarios, respectively, whereas those with $minage_{hab} \geq 30$ years met the target in only 21% and 14% of scenarios. Metapopulation persistence declined with increasing habitat conversion rates and greater habitat age thresholds (Figure 3). Sensitivity analysis indicated that this target was most strongly influenced by $minage_{hab}$ (22% variance explained), $N_{impacted}$ (21% variance explained), and hir (18% variance explained) for persistent colonizers (Appendix S7). For successional specialists, the strongest drivers were ccp (30% variance explained), $minage_{hab}$ (18% variance explained), and $N_{impacted}$ (17% variance explained) (Appendix S7). Notably, although both colonizer types were sensitive to rapid habitat conversion, persistence of successional specialists declined under long conservation commitment periods (Appendix S8), consistent with their inability to colonize mature habitat. The metapopulation recovery target was met in 55% of the simulation scenarios for persistent colonizers and 16% for successional specialists.

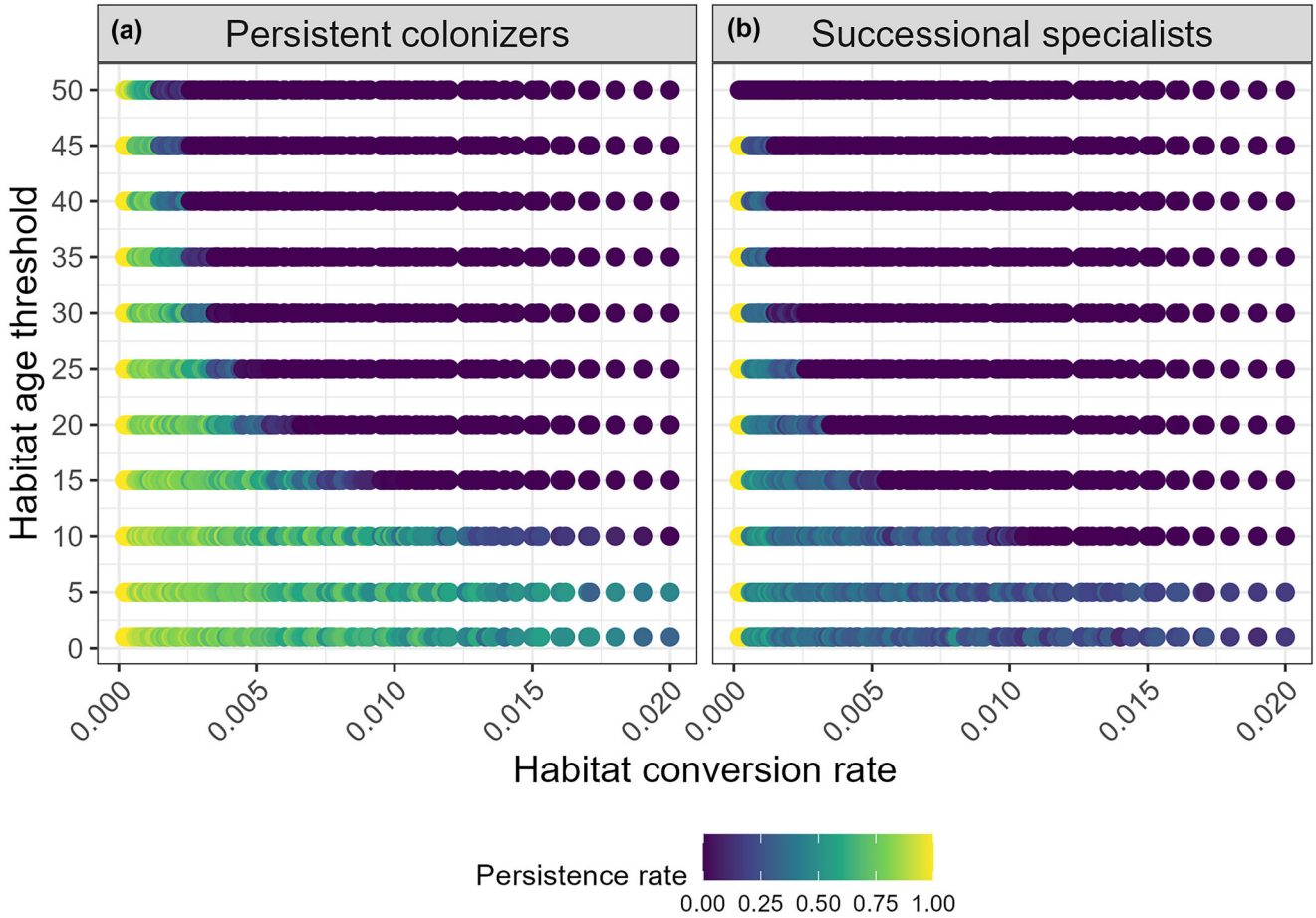

FIGURE 3 Habitat conversion drives the local and regional persistence of habitat-dependent colonizer species across restored patches. The simulated success rates of metapopulation persistence for ecological compensation scenarios with different combinations of habitat conversion rates (the product of the two parameters number of impacted patches and habitat impact ratio) for (a) persistent colonizers (species in young and mature forest patches) and (b) successional specialists (species not capable of occupying mature forest patches ≥100 years old). The simulations underlying each point vary also in other parameters (detailed in MATERIALS AND METHODS).

Limits of biodiversity offsets under high habitat conversion rates

Given that the hcf and ccp emerged as key drivers of long-term offset outcomes, we summarized target achievement rates across all hcf–ccp combinations, spanning the range of scenarios varying the other parameters. Target achievement declined consistently with increasing habitat conversion rate and increasing stringency of target combinations (Figure 4).

High achievement rates (≥95%) for the 95% habitat quality target alone occurred across a defined region of parameter space, requiring approximately hcf ≥1.5 and ccp ≥30 years under low conversion rates and hcf ≥4 and ccp ≥75 years under medium conversion rates; under high conversion rates, high achievement levels were not observed. Ensuring simultaneous achievement of both the habitat quality and matureness targets (i.e., 95% mature patches and mature patch recovery) further reduced the frequency of successful outcomes, with success largely restricted to higher hcf values (≥7.5) and ccps ≥45 years under low conversion rates (Figure 4). When metapopulation targets were added, achievement probabilities declined with increasing habitat conversion rates: maximum achievement rates for any hcf–ccp combination under high conversion rates and with metapopulation targets included reached only 61%. Although the relative ranking of parameter combinations remained broadly consistent across habitat conversion levels for any given target combinations (Spearman correlations 0.61–0.81) (Figure 4), increasing habitat conversion systematically shifted the feasibility boundary by increasing the hcps required to achieve comparable outcomes. Thus, conversion rate reduced overall achievement probabilities while also inflating spatial scaling requirements rather than leaving optimal parameter regions unchanged.

DISCUSSION

Biodiversity offsetting is increasingly used to reconcile development with conservation objectives, yet its long-term effectiveness remains uncertain because ecological recovery occurs

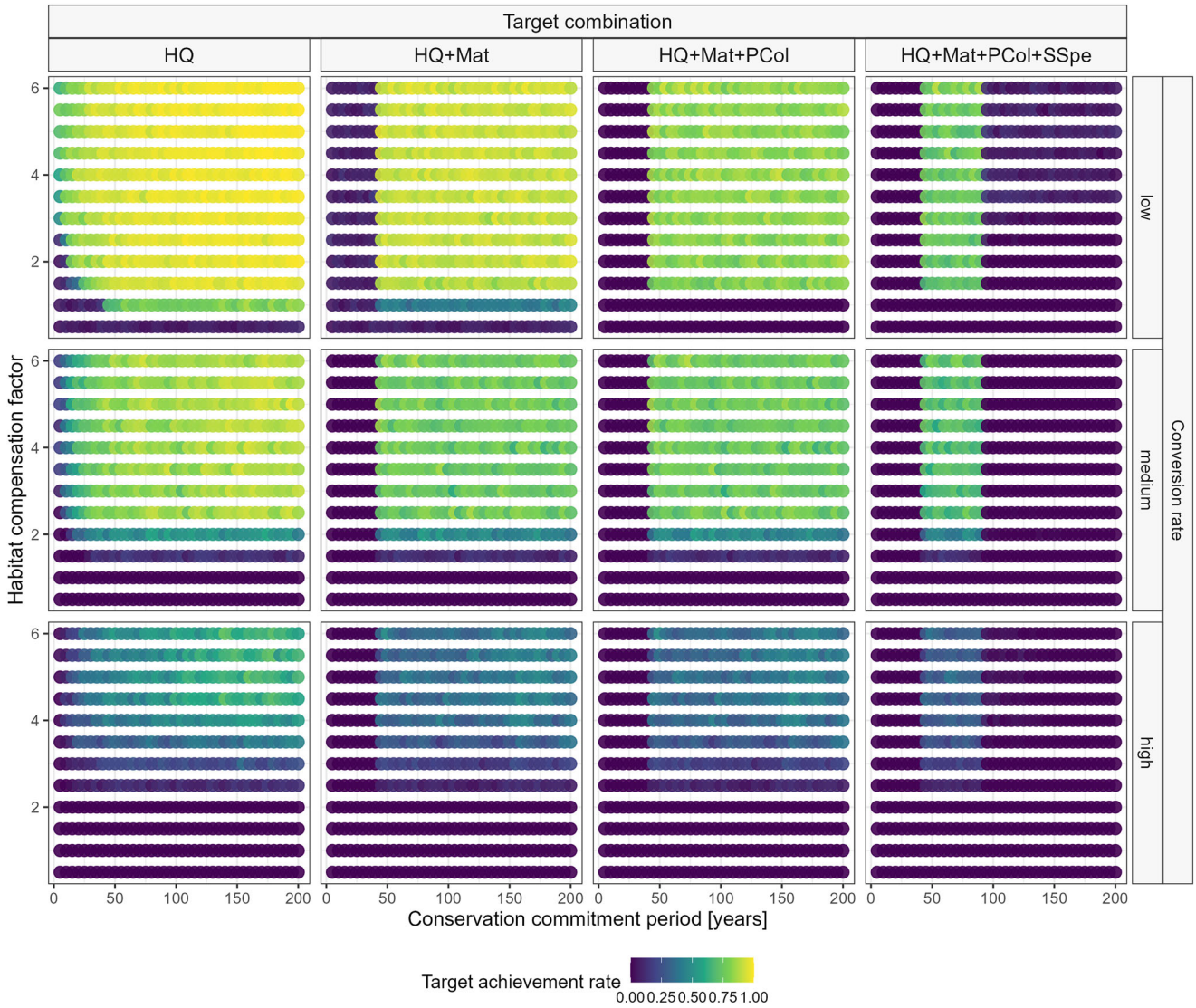

FIGURE 4 Overall target achievement rates across ecological compensation scenarios varying conservation commitment period and habitat compensation factor for cumulative combinations of offset targets: HQ: achieving ≥95% habitat quality target; HQ + Mat: habitat quality combined with ≥95% mature patch ratio or mature patch recovery; HQ + Mat + PCol: previous targets plus ≥95% metapopulation persistence or recovery for persistent colonizer species; and Int + Mat + PCol + SSpe: all prior targets plus ≥95% metapopulation persistence or recovery for successional specialist species. Overall target achievement rates are plotted for three different levels of effective habitat conversion rate per time step (three equally size groups: low, medium, and high). The simulations underlying each point vary also in other parameters as detailed in MATERIALS AND METHODS.

over timescales that often exceed policy and planning horizons. Using a conceptual modeling framework that integrated habitat succession, metapopulation dynamics, and iterative development–offset cycles, we identified four interacting key drivers that determine offset outcomes: spatial compensation scale, conservation commitment duration, habitat conversion rate, and structural constraints imposed by land availability. Our simulations revealed that offset success depended on the interaction between landscape composition turnover and ecological recovery processes that produce delayed responses and long-term dynamics that are not captured by static or short-term evaluations. Furthermore, these outcomes were modulated by species traits and metapopulation dynamics, reflecting differences in recolonization ability and persistence requirements. Critically, required compensation levels were not necessarily fixed but shifted systematically with increasing rates of habitat conversion: faster habitat conversion and landscape turnover reduced overall achievement probabilities and inflated the spatial scaling required to maintain biodiversity targets. Although increasing compensation area and conservation duration improved outcomes, appropriate scaling alone did not guarantee success if habitat conversion outpaced ecological recovery. These results highlighted a fundamental temporal mismatch between ecological processes and conventional offset design, suggesting that effective policies must explicitly account for succession dynamics, landscape turnover rates, and

species-specific recolonization processes rather than relying on simplified area-based metrics or short-term performance criteria. Moreover, reliance on single biodiversity indicators, such as habitat quality alone, risks overlooking metapopulation dynamics and the persistence requirements of habitat-dependent colonizer species. Collectively, our findings indicated that long-term ecological resilience depends on maintaining sufficient mature habitat to sustain recolonization while designing offset strategies that reflect dynamic landscape change.

Offsetting success emerges from temporal dynamics rather than fixed design parameters

Our results showed that offset effectiveness was governed primarily by temporal dynamics arising from the interaction between habitat loss and ecological succession. Because offsetting replaced mature habitats with early successional restoration sites, temporal deficits in habitat quality were unavoidable. Successful outcomes therefore required sufficient spatial and temporal buffering, which were achieved through appropriate scaling of compensation area and conservation commitment duration (whose effects interacted with each other and with additional model parameters), thereby allowing restoration sites to mature and maintain functioning habitat networks. In our simulations, effective offsetting emerged only when conservation commitments extended to ≥45 years, reflecting the successional age difference between removed mature habitat and newly established restoration sites. This outcome suggested that in some modeled scenarios, conservation commitments did not need to extend substantially beyond the period required to maintain landscape-level habitat quality and mature habitat availability, provided that spatial compensation was sufficiently large and habitat conversion rates remained low. Although this finding may appear to challenge expectations that long-term conservation permanence is necessary for ecological resilience (Reside et al., 2019), our results indicated that duration requirements are context dependent; conservation commitments sufficient under low-impact scenarios may become inadequate as habitat conversion intensifies.

Compensation factor thresholds were strongly contingent on habitat conversion rates, highlighting the limitations of fixed ratios. Although a compensation factor of 1 was sometimes sufficient to meet habitat quality targets, substantially higher values (e.g., hcf ≥7.5) were often required to simultaneously maintain habitat quality and mature patch availability. This threshold illustrated that like-for-like area replacement alone cannot compensate for temporal losses in ecosystem structure and function. Under iterative impact–offset cycles, rapid habitat conversion combined with slow ecological recovery generated persistent shortages of mature habitat, leading to structurally and functionally degraded habitat conditions, thereby constraining metapopulation persistence and affecting both habitat-forming and colonizer species.

These results reinforced the mitigation hierarchy, which prioritizes avoidance of impacts, followed by minimization, restoration, and finally offsets, by demonstrating that avoiding habitat loss through low-impact development was the most effective route to landscape-scale NLL. High habitat conversion rapidly increased compensation requirements and could render offsets infeasible, even with large offset areas and long commitment periods (Figure 4). This finding underscored the concept that offsets cannot replace impact avoidance and must be integrated with broader land-use and conservation policies.

Increasing habitat conversion rates systematically shifted feasibility boundaries by increasing the compensation required to achieve comparable outcomes (Figure 4). Offset thresholds therefore represented moving targets determined by the balance between habitat loss and ecological recovery rather than universal benchmarks. Policies relying solely on fixed ratios or static area-based metrics may consequently fail under high development pressure. These findings highlighted a potential mismatch between ecological requirements and current policy frameworks, where conservation durations may be shorter than ecological recovery timescales (e.g., 30-year covenants under the UK Environment Act 2021). Consistent with the results of previous studies (Moilanen et al., 2009; Waddell et al., 2024; Watts et al., 2020), the findings of this study showed that neglecting ecological time lags can undermine long-term biodiversity outcomes. Although our model was parameterized for forest ecosystems with recovery trajectories spanning decades to centuries (Fuentes-Montemayor et al., 2021), the underlying mechanism is broadly applicable; wherever restoration trajectories lag behind habitat loss, spatial overcompensation and long-term protection are necessary to sustain habitat quality and biodiversity. For example, evidence from grassland systems, where structural and functional recovery may require decades despite shorter generation times (Fagan et al., 2008; Hirayama et al., 2025; Redhead et al., 2014; Török et al., 2021; Woodcock et al., 2012), suggests that similar temporal mismatches are likely across different ecosystems.

Species traits and metapopulation processes mediate offset outcomes

Landscape-level dynamics behaved differently for different colonizer species, emphasizing that offset effectiveness cannot be evaluated independent of species-specific ecological traits. Species with higher habitat age thresholds were particularly vulnerable to increased habitat turnover, reflecting their dependence on mature habitat availability and continuous recolonization pathways. Persistent colonizers benefited from remnant or protected habitats acting as sources during periods of reduced habitat availability, which is consistent with metapopulation theory, whereas successional specialists that were assumed to be absent from mature habitats experienced reduced persistence (Figure 3).

Our results demonstrated that constraints in the availability of both mature and early successional habitats can create contrasting outcomes across species groups. Long conservation commitments, although beneficial for maintaining mature habitat, could disadvantage early successional specialists in simplified model landscapes; however, in real-world landscapes,

many species are adapted to additional landscape features and matrix habitats such as treefall gaps and other perturbations within forest habitats, forest margins, or hedgerows (Bengtsson et al., 2000; Montgomery et al., 2020; Turner, 2010), suggesting that such trade-offs may be moderated in practice.

Across scenarios, metapopulation species with higher habitat age thresholds were less likely to persist under faster habitat conversion rates (Figure 3). Species persistence depended on maintaining sufficient numbers of mature patches to prevent landscape-scale bottlenecks that disrupt colonization dynamics. Rapid habitat conversion, coupled with slow restoration implementation, can result in a deficit of mature or remnant habitats, thereby jeopardizing the persistence of habitat-dependent colonizer species reliant on metapopulation dynamics across habitat patches of diverse and specific successional stages for persistence (Hodgson et al., 2009). The higher persistence rates of the habitat-dependent colonizer species (persistent colonizers) compared with those of the successional specialists highlighted the critical role of protected areas because they were not affected by habitat turnover and thus supported spatial dispersal and species persistence. More broadly, if habitat replacement and successional dynamics significantly reduce the availability of suitable habitats for species, alternative habitats such as protected areas may provide a rescue effect during periods of limited habitat availability. These areas can act as sources for recolonization once restoration sites reach a suitable successional stage, a phenomenon that is well known in the ecological literature (Freckleton & Watkinson, 2002; Harrison & Taylor, 1997; Thomas & Kunin, 1999).

Our finding that colonizer species that are dependent on habitat patches for survival are at risk of severe declines if habitat conversion is not buffered by sufficient availability of remnant nearby habitats is consistent with empirical evidence that expansive habitat loss can significantly reduce biodiversity at patch and landscape scales (Gonçalves-Souza et al., 2025; Jamoneau et al., 2012). Therefore, the design of effective offsetting schemes must consider the broader consequences of landscape-scale impacts.

Structural limits imposed by land availability and land-use constraints

Beyond ecological dynamics, our simulations revealed structural limits arising from land availability and competing production demands. Marginal land suitable for offsetting became exhausted in many scenarios, particularly under land availability constraints, preventing further compensation actions. This finding reinforces previous work identifying land availability as a critical constraint on offset feasibility (Sonter et al., 2020).

In actual landscapes, uncertainty surrounding land availability potential, agricultural intensification, and alternative land-use systems complicates implementation of offsetting strategies (Grass et al., 2021; Marshall et al., 2022; McDougall et al., 2019). Even when trade-offs among compensation scale, conservation duration, and production intensity allowed optimization within certain parameter ranges, successful offsetting was not guaranteed where sufficient land for restoration was unavailable. In practice, the risk of exhausting marginal land for offsetting highlights the need to adapt impact and compensation policies to real-world and real-time constraints on land availability.

Temporal dynamics further complicated policy evaluation. Some scenarios meeting short-term targets failed over longer timescales due to gradual declines in biodiversity indicators, whereby failure to meet the offset targets was only evident over time periods >10 years in some scenarios. Other scenarios exhibited transient declines followed by recovery as evidenced by the fact that in some scenarios, both the number of mature patches and metapopulation occupancy ratios declined before eventually recovering. These findings demonstrated that short evaluation windows (e.g., 5–10 years, typically aligned with legislative cycles) may misrepresent long-term ecological outcomes and highlighted the importance of long-term policy and planning considerations aligned with ecological timescales.

Implications for biodiversity offset policy and future research

Collectively, our findings suggest that effective offsetting requires moving beyond static compensation frameworks toward adaptive approaches that explicitly incorporate succession dynamics, land availability constraints, landscape turnover rates, and species-specific persistence mechanisms. Fixed offset ratios are unlikely to ensure biodiversity outcomes across varying ecological and development contexts; instead, policies may benefit from defining feasibility or ecological thresholds that reflect dynamic system constraints.

Our work supports previous studies that highlight the need for sustainable offsetting that accounts for the multifaceted aspects of biodiversity and ecosystem functioning and that implements a whole ecosystem approach, an effort rarely addressed in existing policy (Bullock et al., 2022; Fagan et al., 2010; Maron et al., 2025; Säterberg et al., 2013). Considering multiple species traits and biodiversity indicators is essential, as reliance on single metrics risks overlooking critical dynamics. This real-world policy challenge mirrors a fundamental technical challenge and methodological trade-off in modeling between multidimensional scenarios and simplified scenarios; although multidimensional analyses require consideration of many interacting parameters that may influence outcomes, constrained and simplified designs with only a few parameters allow for easier interpretation but may overlook important dynamics. This modeling challenge has a direct analog in policy: relying on too few ecological indicators can result in misleading assessments of offsetting success. At the same time, fully capturing biodiversity's multifaceted nature is hampered by ecosystem complexity, limited data on the many dimensions of biodiversity and ecosystem functioning, and challenges related to identifying suitable representative indicators (Hughes et al., 2020; Rounsevell et al., 2020; Simmonds et al., 2020).

Several limitations warrant consideration. Our study did not consider the ecological value of marginal patches, which could be relevant in counterfactual scenarios where establish-

ing offsetting sites solely for the purpose of compensating impact elsewhere could mean a loss of biodiversity values from marginal land (Maron et al., 2018). For simplicity, we kept the age of habitat patches constant, although in reality, habitats such as managed forest are subject to both harvest and succession. Such dynamics would further increase heterogeneity in habitat age structure and would be expected to reduce the proportion of mature habitat in the landscape if sufficiently mature habitats would be harvested and replanted for commercial purposes. A previous study suggested that in a European beech forest, landscape mosaic heterogeneity with differently aged forest patches was more important than high within-stand heterogeneity for maintaining regional biodiversity (Schall et al., 2018). Another work based on a large number of differently aged woodlands in the United Kingdom found that management for increased structural complexity may enhance the establishment of woodland plants (Waddell et al., 2024), whereby the recovery of specialist plant species to their former abundance levels in old-growth forests and an overall forest mature habitat structure are typically only achieved in woodlands over 80 years old (Fuentes-Montemayor et al., 2021; Waddell et al., 2024). To our knowledge, however, the role of habitat mosaics and habitat heterogeneity, particularly under conditions of high habitat turnover driven by impact-offsetting in rapidly developing areas, remains largely unexplored and warrants further research.

By integrating habitat succession, metapopulation dynamics, species traits, and iterative landscape-scale development processes, our study demonstrated that biodiversity offset outcomes are fundamentally shaped by temporal dynamics and landscape turnover rather than by fixed compensation thresholds. Achieving a balance between development and conservation requires offset designs that align spatial and temporal scaling with ecological recovery processes while maintaining sufficient mature habitat to sustain recolonization dynamics. Recognizing these constraints is essential for developing offset policies capable of delivering long-term biodiversity outcomes under ongoing landscape change.

AUTHOR CONTRIBUTIONS

K.W. conceived the study, developed the conceptual model, coded the simulation, and wrote the original draft. J.M.B., L.B., M.L., and K.W. interpreted the findings and contributed to manuscript writing and revisions. All authors provided feedback and approved the final version.

ACKNOWLEDGMENTS

K. Wells was in part supported by the Royal Society research grant RGS\R2\222152 and the British Ecological Society research grant SR23\1463. J.B. was supported by the UKRI Natural Environment Research Council (NERC) grant NE/V006525/1. We thank C. Dormann for comments on an earlier draft.

ORCID

Konstans Wells https://orcid.org/0000-0003-0377-2463
Luca Börger https://orcid.org/0000-0001-8763-5997
Miguel Lurgi https://orcid.org/0000-0001-9891-895X
Kevin Watts https://orcid.org/0000-0002-1832-9475
James M. Bullock https://orcid.org/0000-0003-0529-4020

REFERENCES

Balmford, A., Keshav, S., Venmans, F., Coomes, D., Groom, B., Madhavapeddy, A., & Swinfield, T. (2023). Realizing the social value of impermanent carbon credits. *Nature Climate Change*, *13*(11), 1172–1178. https://doi.org/10.1038/s41558-023-01815-0

Bauld, J., Guy, M., Hughes, S., Forster, J., & Watts, K. (2023). Assessing the use of natural colonization to create new forests within temperate agriculturally dominated landscapes. *Restoration Ecology*, *31*(8), Article e14004. https://doi.org/10.1111/rec.14004

Bengtsson, J., Nilsson, S. G., Franc, A., & Menozzi, P. (2000). Biodiversity, disturbances, ecosystem function and management of European forests. *Forest Ecology and Management*, *132*, 39–50. https://doi.org/10.1016/S0378-1127(00)00378-9

Bull, J. W., Gordon, A., Watson, J. E. M., & Maron, M. (2016). Seeking convergence on the key concepts in 'no net loss' policy. *Journal of Applied Ecology*, *53*(6), 1686–1693. https://doi.org/10.1111/1365-2664.12726

Bull, J. W., & Strange, N. (2018). The global extent of biodiversity offset implementation under no net loss policies. *Nature Sustainability*, *1*(12), 790–798. https://doi.org/10.1038/s41893-018-0176-z

Bullock, J. M., Fuentes-Montemayor, E., McCarthy, B., Park, K., Hails, R. S., Woodcock, B. A., Watts, K., Corstanje, R., & Harris, J. (2022). Future restoration should enhance ecological complexity and emergent properties at multiple scales. *Ecography*, *2022*(4), Article e05780. https://doi.org/10.1111/ecog.05780

Buschke, F., & Brownlie, S. (2020). Reduced ecological resilience jeopardizes zero loss of biodiversity using the mitigation hierarchy. *Nature Ecology & Evolution*, *4*(6), 815–819. https://doi.org/10.1038/s41559-020-1177-7

Chazdon, R. L., Falk, D. A., Banin, L. F., Wagner, M., Wilson, S. J., Grabowski, R. C., & Suding, K. N. (2024). The intervention continuum in restoration ecology: Rethinking the active–passive dichotomy. *Restoration Ecology*, *32*(8), e13535. https://doi.org/10.1111/rec.13535

Crouzeilles, R., Ferreira, M. S., Chazdon, R. L., Lindenmayer, D. B., Sansevero, J. B. B., Monteiro, L., Iribarrem, A., Latawiec, A. E., & Strassburg, B. B. N. (2017). Ecological restoration success is higher for natural regeneration than for active restoration in tropical forests. *Science Advances*, *3*(11), Article e1701345. https://doi.org/10.1126/sciadv.1701345

Díaz, S., Settele, J., Brondízio, E. S., Ngo, H. T., Agard, J., Arneth, A., Balvanera, P., Brauman, K. A., Butchart, S. H. M., Chan, K. M. A., Garibaldi, L. A., Ichii, K., Liu, J., Subramanian, S. M., Midgley, G. F., Miloslavich, P., Molnár, Z., Obura, D., Pfaff, A., … Zayas, C. N. (2019). Pervasive human-driven decline of life on Earth points to the need for transformative change. *Science*, *366*(6471), Article eaax3100. https://doi.org/10.1126/science.aax3100

Dobson, A. D. M., Bradfer-Lawrence, T., Finch, T., Hanley, N., Fuentes-Montemayor, E., Nthambi, M., Simpson, K., Watts, K., & Park, K. J. (2025). Combining occupancy and dispersal models to predict the conservation benefits of land-use change. *Landscape Ecology*, *40*(4), Article 75. https://doi.org/10.1007/s10980-025-02087-z

Fagan, K. C., Pywell, R. F., Bullock, J. M., & Marrs, R. H. (2010). Are ants useful indicators of restoration success in temperate grasslands? *Restoration Ecology*, *18*(3), 373–379. https://doi.org/10.1111/j.1526-100X.2008.00452.x

Fagan, K. C., Pywell, R. F., Bullock, J. M., & Marrs, R. H. (2008). Do restored calcareous grasslands on former arable fields resemble ancient targets? The effect of time, methods and environment on outcomes. *Journal of Applied Ecology*, *45*, 1293–1303. https://doi.org/10.1111/j.1365-2664.2008.01492.x

Freckleton, R. P., & Watkinson, A. R. (2002). Large-scale spatial dynamics of plants: Metapopulations, regional ensembles and patchy populations. *Journal of Ecology*, *90*(3), 419–434. https://doi.org/10.1046/j.1365-2745.2002.00692.x

Fuentes-Montemayor, E., Park, K. J., Cordts, K., & Watts, K. (2021). The long-term development of temperate woodland creation sites: From tree saplings to mature woodlands. *Forestry: An International Journal of Forest Research*, *95*(1), 28–37. https://doi.org/10.1093/forestry/cpab027

Gibbons, P., Macintosh, A., Constable, A. L., & Hayashi, K. (2018). Outcomes from 10 years of biodiversity offsetting. *Global Change Biology*, *24*(2), e643–e654. https://doi.org/10.1111/gcb.13977

Gonçalves-Souza, T., Chase, J. M., Haddad, N. M., Vancine, M. H., Didham, R. K., Melo, F. L. P., Aizen, M. A., Bernard, E., Chiarello, A. G., Faria, D., Gibb, H., de Lima, M. G., Magnago, L. F. S., Mariano-Neto, E., Nogueira, A. A., Nemésio, A., Passamani, M., Pinho, B. X., Rocha-Santos, L., … Sanders, N. J. (2025). Species turnover does not rescue biodiversity in fragmented landscapes. *Nature*, *640*, 702–706. https://doi.org/10.1038/s41586-025-08688-7

Grass, I., Batáry, P., & Tscharntke, T. (2021). Combining land-sparing and land-sharing in European landscapes. In *Advances in Ecological Research*. (pp. 251–303) (eds. D. A. Bohan, & A. J. Vanbergen). Academic Press.

Griscom, B. W., Adams, J., Ellis, P. W., Houghton, R. A., Lomax, G., Miteva, D. A., Schlesinger, W. H., Shoch, D., Siikamäki, J. V., Smith, P., Woodbury, P., Zganjar, C., Blackman, A., Campari, J., Conant, R. T., Delgado, C., Elias, P., Gopalakrishna, T., Hamsik, M. R., … Fargione, J. (2017). Natural climate solutions. *Proceedings of the National Academy of Sciences*, *114*(44), 11645–11650. https://doi.org/10.1073/pnas.1710465114

Harrison, S., & Taylor, A. D. (1997). Empirical evidence for metapopulation dynamics. In I. Hanski & M. E. Gilpin (Eds.), *Metapopulation biology* (pp. 27–42). Academic Press.

Hirayama, G. S., Inoue, T., Kenta, T., Ishii, H. S., & Ushimaru, A. (2025). Long-term management is required for the recovery of pollination networks and function in restored grasslands. *Journal of Applied Ecology*, *62*, 814–823. https://doi.org/10.1111/1365-2664.70017

Hodgson, J. A., Moilanen, A., & Thomas, C. D. (2009). Metapopulation responses to patch connectivity and quality are masked by successional habitat dynamics. *Ecology*, *90*(6), 1608–1619.

Hughes, A. C., Qiao, H., & Orr, M. C. (2020). Extinction targets are not SMART (specific, measurable, ambitious, realistic, and time bound). *Bioscience*, *71*(2), 115–118. https://doi.org/10.1093/biosci/biaa148

Jamoneau, A., Chabrerie, O., Closset-Kopp, D., & Decocq, G. (2012). Fragmentation alters beta-diversity patterns of habitat specialists within forest metacommunities. *Ecography*, *35*(2), 124–133. https://doi.org/10.1111/j.1600-0587.2011.06900.x

Kalliolevo, H., Pérez Chaves, P., Hamedani Raja, P., Vuorisalo, T., & Bull, J. W. (2025). Rewilding for biodiversity offsets: A case study of passive ecological restoration on lowland agricultural land for Biodiversity Net Gain in England. *Global Ecology and Conservation*, *60*, Article e03603. https://doi.org/10.1016/j.gecco.2025.e03603

Leclère, D., Obersteiner, M., Barrett, M., Butchart, S. H. M., Chaudhary, A., De Palma, A., DeClerck, F. A. J., Di Marco, M., Doelman, J. C., Dürauer, M., Freeman, R., Harfoot, M., Hasegawa, T., Hellweg, S., Hilbers, J. P., Hill, S. L. L., Humpenöder, F., Jennings, N., Krisztin, T., … Young, L. (2020). Bending the curve of terrestrial biodiversity needs an integrated strategy. *Nature*, *585*, 551–556. https://doi.org/10.1038/s41586-020-2705-y

Maron, M., von Hase, A., Quétier, F., Sonter, L. J., Theis, S., & zu Ermgassen, S. O. S. E. (2025). Biodiversity offsets, their effectiveness and their role in a nature positive future. *Nature Reviews Biodiversity*, *1*, 183–196. https://doi.org/10.1038/s44358-025-00023-2

Maron, M., Brownlie, S., Bull, J. W., Evans, M. C., von Hase, A., Quétier, F., Watson, J. E. M., & Gordon, A. (2018). The many meanings of no net loss in environmental policy. *Nature Sustainability*, *1*, 19–27. https://doi.org/10.1038/s41893-017-0007-7

Marshall, E., Visintin, C., Valavi, R., Wilkinson, D. P., Southwell, D., Wintle, B. A., & Kujala, H. (2022). Integrating species metrics into biodiversity offsetting calculations to improve long-term persistence. *Journal of Applied Ecology*, *59*, 1060–1071. https://doi.org/10.1111/1365-2664.14117

Martin, P. A., Newton, A. C., & Bullock, J. M. (2013). Carbon pools recover more quickly than plant biodiversity in tropical secondary forests. *Proceedings of the Royal Society B: Biological Sciences*, *280*(1773). Article 20132236. https://doi.org/10.1098/rspb.2013.2236

McDougall, R., Kristiansen, P., & Rader, R. (2019). Small-scale urban agriculture results in high yields but requires judicious management of inputs to achieve sustainability. *Proceedings of the National Academy of Sciences*, *116*, 129–134. https://doi.org/10.1073/pnas.1809707115

Moilanen, A., Van Teeffelen, A. J. A., Ben-Haim, Y., & Ferrier, S. (2009). How much compensation is enough? A framework for incorporating uncertainty and time discounting when calculating offset ratios for impacted habitat. *Restoration Ecology*, *17*(4), 470–478. https://doi.org/10.1111/j.1526-100X.2008.00382.x

Montgomery, I., Caruso, T., & Reid, N. (2020). Hedgerows as Ecosystems: Service Delivery, Management, and Restoration. *Annual Review of Ecology, Evolution, and Systematics*, *51*, 81–102. https://doi.org/10.1146/annurev-ecolsys-012120-100346

Piovesan, G., & Biondi, F. (2021). On tree longevity. *New Phytologist*, *231*(4), 1318–1337. https://doi.org/10.1111/nph.17148

Planque, B., Aarflot, J. M., Buttay, L., Carroll, J., Fransner, F., Hansen, C., Husson, B., Langangen, Ø., Lindstrøm, U., Pedersen, T., Primicerio, R., Sivel, E., Skogen, M. D., Strombom, E., Stige, L. C., Varpe, Ø., & Yoccoz, N. G. (2022). A standard protocol for describing the evaluation of ecological models. *Ecological Modelling*, *471*, Article 110059. https://doi.org/10.1016/j.ecolmodel.2022.110059

Pretzsch, H. (2009). *Forest dynamics, growth and yield: From measurement to model*. Springer.

R Core Team. (2024). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. http://www.R-project.org

Redhead, J. W., Sheail, J., Bullock, J. M., Ferreruela, A., Walker, K. J., & Pywell, R. F. (2014). The natural regeneration of calcareous grassland at a landscape scale: 150 years of plant community re-assembly on Salisbury Plain, UK. *Applied Vegetation Science*, *17*, 408–418. https://doi.org/10.1111/avsc.12076

Reside, A. E., Briscoe, N. J., Dickman, C. R., Greenville, A. C., Hradsky, B. A., Kark, S., Kearney, M., Kutt, A. S., Nimmo, D., Pavey, C. R., Read, J., Ritchie, E. G., Roshier, D. A., Skroblin, A., Stone, Z., West, M., & Fisher, D. O. (2019). Persistence through tough times: Fixed and shifting refuges in threatened species conservation. *Biodiversity and Conservation*, *28*, 1303–1330. https://doi.org/10.1007/s10531-019-01734-7

Rounsevell, M. D. A., Harfoot, M., Harrison, P. A., Newbold, T., Gregory, R. D., & Mace, G. M. (2020). A biodiversity target based on species extinctions. *Science*, *368*(6496), 1193–1195. https://doi.org/10.1126/science.aba6592

Säterberg, T., Sellman, S., & Ebenman, B. (2013). High frequency of functional extinctions in ecological networks. *Nature*, *499*(7459), 468–470. https://doi.org/10.1038/nature12277

Schall, P., Gossner, M. M., Heinrichs, S., Fischer, M., Boch, S., Prati, D., Jung, K., Baumgartner, V., Blaser, S., Böhm, S., Buscot, F., Daniel, R., Goldmann, K., Kaiser, K., Kahl, T., Lange, M., Müller, J., Overmann, J., Renner, S. C., … Ammer, C. (2018). The impact of even-aged and uneven-aged forest management on regional biodiversity of multiple taxa in European beech forests. *Journal of Applied Ecology*, *55*(1), 267–278. https://doi.org/10.1111/1365-2664.12950

Seddon, N., Chausson, A., Berry, P., Girardin, C. A. J., Smith, A., & Turner, B. (2020). Understanding the value and limits of nature-based solutions to climate change and other global challenges. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *375*(1794), Article 20190120. https://doi.org/10.1098/rstb.2019.0120

Simmonds, J. S., Sonter, L. J., Watson, J. E. M., Bennun, L., Costa, H. M., Dutson, G., Edwards, S., Grantham, H., Griffiths, V. F., Jones, J. P. G., Kiesecker, J., Possingham, H. P., Puydarrieux, P., Quétier, F., Rainer, H., Rainey, H., Roe, D., Savy, C. E., Souquet, M., … Maron, M. (2020). Moving from biodiversity offsets to a target-based approach for ecological compensation. *Conservation Letters*, *13*(2), Article e12695. https://doi.org/10.1111/conl.12695

Sonter, L. J., Simmonds, J. S., Watson, J. E. M., Jones, J. P. G., Kiesecker, J. M., Costa, H. M., Bennun, L., Edwards, S., Grantham, H. S., Griffiths, V. F., Jones, K., Sochi, K., Puydarrieux, P., Quétier, F., Rainer, H., Rainey, H., Roe, D., Satar, M., Soares-Filho, B. S., … Maron, M. (2020). Local conditions and policy design determine whether ecological compensation can achieve No Net Loss goals. *Nature Communications*, *11*(1), Article 2072. https://doi.org/10.1038/s41467-020-15861-1

Swinfield, T., Shrikanth, S., Bull, J. W., Madhavapeddy, A., & zu Ermgassen, S. O. S. E. (2024). Nature-based credit markets at a crossroads. *Nature Sustainability*, *7*(10), 1217–1220. https://doi.org/10.1038/s41893-024-01403-w

Török, P., Brudvig, L. A., Kollmann, J., Price, J. N., & Tóthmérész, B. (2021). The present and future of grassland restoration. *Restoration Ecology*, *29*, e13378. https://doi.org/10.1111/rec.13378

Thomas, C. D., & Kunin, W. E. (1999). The spatial structure of populations. *Journal of Animal Ecology*, *68*(4), 647–657.

Turner, M. G. (2010). Disturbance and landscape dynamics in a changing world. *Ecology*, *91*, 2833–2849.

Waddell, E. H., Fuentes-Montemayor, E., Park, K. J., Carey, P., Guy, M., Macgregor, N. A., & Watts, K. (2024). Larger and structurally complex woodland creation sites provide greater benefits for woodland plants. *Ecological Solutions and Evidence*, *5*(2), Article e12339. https://doi.org/10.1002/2688-8319.12339

Watts, K., Whytock, R. C., Park, K. J., Fuentes-Montemayor, E., Macgregor, N. A., Duffield, S., & McGowan, P. J. K. (2020). Ecological time lags and the journey towards conservation success. *Nature Ecology & Evolution*, *4*(3), 304–311. https://doi.org/10.1038/s41559-019-1087-8

Wauchope, H. S., zu Ermgassen, S. O. S. E., Jones, J. P. G., Carter, H., Schulte to Bühne, H., & Milner-Gulland, E. J. (2024). What is a unit of nature? Measurement challenges in the emerging biodiversity credit market. *Proceedings of the Royal Society B: Biological Sciences*, *291*(2036), Article 20242353. https://doi.org/10.1098/rspb.2024.2353

Winkler, K., Fuchs, R., Rounsevell, M., & Herold, M. (2021). Global land use changes are four times greater than previously estimated. *Nature Communications*, *12*(1), Article 2501. https://doi.org/10.1038/s41467-021-22702-2

Woodcock, B. A., Bullock, J. M., Mortimer, S. R., Brereton, T., Redhead, J. W., Thomas, J. A., & Pywell, R. F. (2012). Identifying time lags in the restoration of grassland butterfly communities: A multi-site assessment. *Biological Conservation*, *155*, 50–58. https://doi.org/10.1016/j.biocon.2012.05.013

Wunder, S., Fraccaroli, C., Bull, J. W., Dutta, T., Eyres, A., Evans, M. C., Thorsen, B. J., Jones, J. P. G., Maron, M., Muys, B., Pacheco, A., Olesen, A. S., Swinfield, T., Tegegne, Y. T., White, T. B., Zhang, H., & zu Ermgassen, S. O. S. E. (2025). Biodiversity credits: An overview of the current state, future opportunities, and potential pitfalls. *Business Strategy and the Environment*, *34*(7), 8470–8499. https://doi.org/10.1002/bse.70018

zu Ermgassen, S. O. S. E., Utamiputri, P., Bennun, L., Edwards, S., & Bull, J. W. (2019). The role of "No Net Loss" policies in conserving biodiversity threatened by the global infrastructure boom. *One Earth*, *1*(3), 305–315. https://doi.org/10.1016/j.oneear.2019.10.019

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Wells, K., Börger, L., Lurgi, M., Watts, K., & Bullock, J. M. (2026). Optimizing biodiversity offsetting for habitat succession and colonization dynamics. *Conservation Biology*, e70362. https://doi.org/10.1111/cobi.70362