Adding ecological and evolutionary processes to restoration biodiversity offset models using neutral theory

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Abstract
Aim: Biodiversity offsets are being implemented or planned across all continents and biogeographical realms. Due to their popularity, new offset projects have developed faster than empirical evidence of their ecological effectiveness, so policy has been informed by quantitative models. However, these models have yet to incorporate ecological and evolutionary processes, which vary globally. Here we use the unified neutral theory of biodiversity to integrate speciation and dispersal into models of restoration biodiversity offsets.

Location: A simulated one-dimensional circular landscape.

Methods: We designed a simulation framework based on neutral theory that allowed us to compare restoration biodiversity offsets under various scenarios of speciation, dispersal and offset implementation: no offsets, passive restoration and translocation. This approach allowed us to evaluate time series of multiple metrics of biodiversity (richness, evenness and community similarity) at different spatial scales (patch and landscape), which were then compared using model-based recursive partitioning.

Results: The choice of offset implementation was the main determinant of successful offset outcomes; translocation consistently had the best outcomes. Passive restoration only improved offset outcomes for systems with high speciation rates. Speciation and dispersal mainly played a secondary role in offset outcomes, with dispersal only affecting offset outcomes at landscape scales. Outcomes also varied across different metrics of biodiversity, with species richness and evenness showing opposing trajectories for some scenarios.

Main conclusions: Although ecological and evolutionary processes affect biodiversity offset outcomes, the type of offset implementation remains the most important determinant of offset success. This emphasizes the development—and effective implementation—of robust offset policies and guidelines that include active translocation and demand more than just passive restoration.

Keywords: biodiversity offsets, community dissimilarity, evenness, mitigation, neutral theory, no net loss, restoration, richness, translocation
Biodiversity offsetting is gaining popularity globally as a mechanism to compensate for the loss of biodiversity at one locality with an equivalent gain elsewhere (Bull, Suttle, Gordon, Singh, & Milner-Gulland, 2013). Currently, 70 countries have policies that regulate biodiversity offsets in place or under development, covering all continents and terrestrial biogeographical realms except Antarctica (Holt et al., 2013; Maron et al., 2016). There are many potential issues with biodiversity offsets (Maron et al., 2016), and perhaps the most challenging is developing approaches that can effectively address the breadth of different ecological and evolutionary circumstances found across the globe.

New offsetting projects are outpacing empirical evidence of their effectiveness, which only appear post-implementation (Gibbons, Macintosh, Constable, & Hayashi, 2018; Lindemayer et al., 2017; May, Hobbett, & Valentine, 2017). Therefore, previous studies of the ecological viability of offsets have relied on quantitative models (Bull, Gordon, Law, Suttle, & Milner-Gulland, 2014; Bull, Hardy, Moilanen, & Gordon, 2015; Gibbons et al., 2015; Latil, Moilanen, & Pouzols, 2014). These models generally simulate biodiversity as a stock that rises or falls according to interacting rates of loss from development, gains from offsets and a natural background biodiversity trajectory. Although these models have provided valuable insights into the general flexibility of offsets, they do not consider explicitly the ecological and evolutionary processes that underpin biodiversity. Instead, like many offset policies, they focus on the emergent properties of biological processes, such as population size or habitat cover, without considering the speciation, births, deaths and migration of individual organisms (Burgin, 2008). Not only are such processes by individual organisms important for the long-term persistence of biodiversity, it is likely that they also determine the impacts of biodiversity offset schemes and other conservation actions (Moreno-Mateos, Maris, Béchet, & Curran, 2015; Pressey, Weeks, & Gurney, 2017; Walker, Brower, Stephens, & Lee, 2009).

Ecological and evolutionary processes likely affect the ecological aspects of offset implementation. For example, like-for-like biodiversity offsets cannot substitute irreplaceable biodiversity with high levels of endemism (Pilgrim et al., 2013). Endemism is the consequence of historical speciation rates (Latimer, Silander, & Cowling, 2005), which vary geographically and across taxonomic groups (Jetz, Thomas, Joy, Hartmann, & Mooers, 2012). Similarly, many offsets rely on habitat restoration, which re-establishes vegetation cover using a few fast-growing plant species with the intention of allowing secondary colonization by species migrating from the habitat matrix (Gómez-Aparicio, 2009; Zaloumis & Bond, 2011). Dispersal rates and, therefore, the likelihood of secondary succession would directly affect offset outcomes. Dispersal rates also vary taxonomically (Nathan & Muller-Landau, 2000; Tuomisto, Ruokolainen, & Yi-Halla, 2003) and geographically (Joquie, Field, Brendonck, & Meester, 2010). Therefore, understanding how these ecological and evolutionary processes affect outcomes is central to implementing offsets successfully across the globe.

In this study, we expand on earlier quantitative biodiversity offset models by incorporating ecological and evolutionary processes using the unified neutral theory of biodiversity (Hubbell, 2001). Neutral theory considers explicitly the speciation, births, deaths and migration of individual organisms, but makes the simplifying assumption that deterministic fitness differences between organisms do not affect patterns of community composition (Hubbell, 2001; Rosindell, Hubbell, & Etienne, 2011). Instead, community patterns are based on random and equiprobable (i.e., neutral) demographic processes. This assumption of demographic equivalence (Munoz & Huneman, 2016) is aligned with the similar assumption of ecological equivalence that underpins many biodiversity offsetting schemes (Quétié & Lavorel, 2011).

Biodiversity summarizes the variation of genes, species communities and ecosystems across multiple spatial scales (Noss, 1990). Neutral theory has the advantage of generating multiple biodiversity patterns at more than one spatial scale (Buschke, Brendonck, & Vanschoenwinkel, 2016; May, Huth, & Wiegand, 2015). For practical reasons, offset policies and models only address specific features of biodiversity and not biodiversity as a whole (Bull, Gordon, Watson, & Maron, 2016). However, it is important that the most appropriate metrics and scales are used to evaluate biodiversity offsets, rather than merely favouring those features that are most easy to quantify (Bull et al., 2016; Burgin, 2008; Pressey et al., 2017). Neutral theory can identify whether the choice of biodiversity metrics has the potential to misrepresent the success or failure of an individual offset and, therefore, the success or failure of offsetting at both national and international scales.

In this study, we use neutral theory to model whether the loss of biodiversity at one locality can be compensated for at a different portion of a simulated landscape and ultimately deliver true net loss. We explore this for different rates of speciation and dispersal, as well as different types of mitigation: no offsets, passive restoration (where the habitat is restored to allow secondary colonization of species from the surrounding matrix) and active restoration (where species from the development site are translocated to the offset site). In general, we anticipate that biodiversity offsets will be less feasible when speciation rates are high, due to the resulting increase in endemism and standing stock of biodiversity; and dispersal rates are low, because dispersal limitation leads to non-substitutable heterogeneous assemblages. Moreover, we expect that these circumstances of high speciation and low dispersal will amplify the differences between offset implementation (passive vs. active restoration).

2 | METHODS

We simulated the dynamics of a one-dimensional and circular landscape made up of 179 habitat patches, which can be imagined as a clock face with a patch every 20 s, or every two degrees (Figure 1). This circular arrangement of an uneven number of patches ensured
that all patches were equally connected to other patches so that no gradients in biodiversity could arise as a result of mid-domain effects (Rangel & Diniz-Filho, 2005). Each of the patches had the capacity to support 100 individuals, regardless of their species identity (thus, the total size of the metacommunity, \( J \), equalled 17,900 individuals).

We simulated the biodiversity dynamics of this landscape under four levels of speciation (\( \nu = 0.00075, 0.0025, 0.005, 0.01 \)), which resemble those from empirical datasets (Table 1), and three levels of dispersal (\( m = 0.25, 0.5, 0.75 \)). Dispersal rates are strongly scale dependent (immigration is much more prominent at smaller spatial scales: McGill, Maurer, & Weiser, 2006), but our dispersal parameters were similar to those of Mountain fynbos in the Cape Floristic Region, South Africa (\( m = 0.27 \): Etienne, Latimer, Silander, & Cowling, 2006), tropical forest at Manu National Park, Peru (\( m = 0.53 \): Etienne et al., 2006), and local scale (<5 ha) tropical trees at Barro Colorado Island, Panama (0.6 < \( m < 0.95 \): McGill et al., 2006).

Here, \( \nu \) can be interpreted as either the formation of new species through speciation or as the colonization of the regional species pool by new species. Nevertheless, we refer to this parameter as speciation throughout the manuscript to be consistent with previous studies of neutral theory (Hubbell, 2001; Rosindell et al., 2011). The speciation parameter, \( \nu \), is related to Hubbell's (2001) fundamental biodiversity number, \( \theta \), because \( \theta = J \times \nu/(1 - \nu) \) in cases with overlapping generations (Rosindell et al., 2011). The dispersal parameter, \( m \), was the probability that an individual immigrated into a patch from a different source patch. The source

**FIGURE 1** Conceptual outline for the simulated landscape for the four offset scenarios. (a) Scenario 1 is the counterfactual where there is neither development nor an offset. (b) Scenario 2 is where biodiversity is lost due to development, but there is no offset. (c) In Scenario 3, biodiversity is lost to development and this is offset by restoring the habitat capacity at the offset site and allowing recolonisation from the surrounding matrix. (d) In Scenario 4, biodiversity is lost to development and is offset by translocating the intact assemblage to the offset site, thereby changing the spatial configuration.

**TABLE 1** The four speciation rates, \( \nu \), used in neutral simulations, their equivalent fundamental biodiversity numbers, \( \theta \), and a selection of published case studies with similar values for \( \theta \).

| Simulated speciation rate (\( \nu \)) | Equivalent fundamental biodiversity number (\( \theta \)) | Comparable real-world cases
---|---|---
0.00075 | 13.4 | Prairie grasslands in Minnesota, USA. (\( \theta \approx 14.94 \): Harpole & Tilman, 2006)
0.0025 | 44.9 | Breeding birds throughout USA (\( \theta \approx 18.46 \): McGill, 2003)
0.005 | 89.9 | Tropical moist forest species at Barro Colorado Island, Panama (\( \theta \approx 48.4 \): Hubbell, 2001; Etienne, 2005)
0.01 | 180.8 | Mountain fynbos in the Cape Floristic Region, South Africa (\( \theta \approx 44.2 \): Etienne et al., 2006)

\( \theta \) was estimated as \( J \times \nu/(1 - \nu) \), where \( J \) is the number of individuals in the simulation. The values are only for illustrative purposes because the exact value of \( \theta \) depends on the sampling formula used (Etienne et al., 2006) as well as the spatial scale of assessment (McGill et al., 2006).
patch was selected from a dispersal kernel based on the inverse-
squared distance between patches; adjacent patches were sepa-
rated by one arbitrary distance unit and, because the gradient was
circular, no patch was ever more than 90 distance units from all
other patches.

In the simulation framework (Figure 1), we first initialized the
assemblage using neutral processes and then simulated the outcomes
of four management scenarios from the same starting assemblage:
(a) no development and no offset counterfactual scenario, (b) devel-
opment without offsets scenario, (c) development with a passive re-

toration offset scenario and (d) development with active restoration
offsets scenario (hereafter referred to as the translocation scenario).
These scenarios were chosen because they represent four points
from a state of no development to a continuum of increasingly ef-
fective mitigation (no mitigation, simple mitigation and perfect miti-
gation). In reality, offsets are implemented to varying degrees along
this continuum (Bull & Strange, 2018) with different levels of success
(Bezombes, Kerbiriou, & Spiegelberger, 2019). Therefore, our sim-
ulated scenarios should be interpreted as archetypes, rather than
faithful representations of all real world circumstances.

The entire process—initialization and scenario modelling—was
iterated 100 times for each combination of speciation and disper-
sal. All simulations were performed in R version 3.3.0 (R Core Team,
2016) through a cloud-based RStudio Server version 0.99.896 run-
ing on Ubuntu 16.04 LTS on an Amazon Machine Image (2.4 GHz
Intel Xeon dual processor).

2.1 | Initializing the simulation

Modelling spatially explicit neutral processes can be computa-
tionally exhaustive, so we used a coalescence approach to initialize the
simulation (Rosindell, Wong, & Etienne, 2008). Coalescence works
by tracing the lineage of individuals in a simulation in a retrospective
manner and, by doing so, ensuring that the assemblage represents a
steady state. Briefly, the coalescence approach selected an individ-
ual randomly at each time step and then assigned it a species iden-
tity. The species identity was determined by setting the individual
on a retrospective random walk. The probability that the individual
arose through speciation was determined by \( \nu \), which then assigned
the individual a unique species identity and removed it for the rest
of the simulation. When the individual did not arise through specia-
tion, then the direction of its random walk was determined by the
dispersal parameter, \( m \), and the dispersal kernel. Once the individual
reached its source patch, a second individual (i.e., the parent) was
randomly selected from the patch and the two individuals were ag-
gregated into the same lineage (i.e., coalesced). A coalesced lineage
was then treated as the same species unit in subsequent time steps.
The coalescence simulation continued until every single individual
was assigned a species identity either through speciation or coales-
cence with other lineages.

After the assemblage was established through coalescence, 20
patches (patches 81–100) were completely cleared of all individuals.
This represented the pre-existing degraded portion of the landscape
that could be used as the offset receiving site in subsequent sim-
ulations. It was necessary to create these offset receiving patches
after setting up the landscape for two reasons: first, we assumed
that most offset receiving sites in practice are degraded due to mod-
ern impacts that are too recent to allow the landscape to reach a new
equilibrium state at ecological and evolutionary time-scales; and,
second, degrading these patches prior to initializing the simulation
would create edge-effects in the circular landscape.

2.2 | Scenario 1: Counterfactual of no
development and no offsets

The counterfactual was the scenario in which no development took
place and no offset was implemented and served as the baseline
against which the other scenarios were measured (Figure 1a). After
the assemblage was initialized through coalescence and the potential
offset receiving patches were cleared, the simulation was allowed
to continue following similar rules of speciation and dispersal for
100,000 time steps. This duration meant that the entire assemblage
could theoretically be replaced between five and six times. Thus, the
length of the simulation would be equivalent to 15–24 years for me-
dium-lived species, such passerine birds (5–6 generations \( \times 3–4 \) year
lifespan), but relatively shorter or longer for short- and long-lived
species, respectively.

At each time step of the simulation, a patch was selected at ran-
dom from which one individual was chosen. Each individual had an
equiprobable chance of being selected, so the probability of any
specific species being selected was determined by its relative abun-
dance. The selected individual would then die by being removed
from the simulation and would be replaced by a birth of a new in-
dividual. The probability that this newly-born individual was from
a species new to the landscape was determined by \( \nu \) and the prob-
ability that it originated from a different patch was \( m \). The species
identity of the new individual was determined by randomly select-
ing a parent individual with equal probability, so the probability of it
belonging to a specific species was, once again, determined by the
relative abundance of that species.

Five diversity patterns were quantified every 1,000 time steps.
The first pattern was local species richness, which was the average
of the number of species in each of the 179 patches. The second
pattern was regional species richness, which was the total number
of unique species across the whole landscape. Pielou’s evenness (Pielou,
1966) quantified how evenly abundances were distributed among
species; with higher evenness suggesting that relative abundances
were more similar among species. Pielou’s evenness is the Shannon
entropy (diversity function in the vegan package) divided by the nat-
ural logarithm of species richness. The average Pielou’s evenness
was calculated for each of the 179 patches (local evenness) as well
as for the whole assemblage (regional evenness). The fifth pattern
was community dissimilarity, which was summarized as the homo-
geney of multivariate dispersion (Anderson, Ellingsen, & McArdle,
2006; betadisper function in the vegan package). Multivariate dis-

erion required the pairwise calculation of Bray–Curtis similarity
between patches. The patches were then projected into a multi-
dimensional space as a cloud of points (i.e., patches), where more
similar patches were closer together and less similar patches further
apart. Community dissimilarity was quantified as the mean distance
of each patch to the centroid of this cloud of points. Thus, the mean
distance to centroid would be small when the assemblage was uni-
formly distributed across the landscape or large if the assemblage
was distributed heterogeneously.

2.3 | Scenario 2: Development without offsets

The simulation for the development without offsets scenario was
identical to the counterfactual scenario with one exception. After
initializing the landscape and clearing the offset receiving sites, but
prior to running the simulation for 100,000 time steps, 20 patches
(patches 1–10 and 170–179) were completely cleared of all individu-
als and the habitat capacity was set to 0 (Figure 1b). This represented
the loss of biodiversity caused by development. Once this diversity
was lost, the simulation continued as described in the counterfactual
with the same five biodiversity patterns recorded every 1,000 time
steps.

2.4 | Scenario 3: Development with passive
restoration

The passive restoration scenario included the same loss of diversity
as described in Scenario 2, but differed in that the habitat capacity
of the offset receiving site (patches 81–100) was restored to 100
individuals. This is equivalent to removing adverse degrading dis-
turbances; remodelling and stabilizing topography as a precursor to
natural revegetation through recolonization from adjacent habitat
patches; or recreating habitat (e.g., ponds, refugia or nesting sites) to
be colonized by animals from elsewhere (Lindenmayer et al., 2017;
Rey Benayas, Newton, Diaz, & Bullock, 2009; Suding, 2011).

In this scenario, the offset receiving site was unoccupied at the
start of the forward simulation, but was open to colonization by in-
dividuals from elsewhere. This required a slight modification to the
birth–death process (following Buschke et al., 2016). As with the
other scenarios, an individual was added to a patch either through
speciation or the birth of a new individual from a source patch (the
probability of with is determined by \( \nu \) and \( m \), respectively). If there
were already 100 individuals in a patch (i.e., the patch was at carrying
capacity), then a death process took place as for the other scenarios
to ensure zero-sum dynamics. If, however, there were fewer than
100 individuals in a patch (i.e., the patch has yet to reach carrying ca-
pacity), then the birth process would proceed without a counter-bal-
ancing death. This process would continue for 100,000 time steps,
and the same five patterns would be quantified every 1,000 steps.

2.5 | Scenario 4: Development with translocation

In this scenario, the assemblage was initialized as in the other scenar-
ios, and development took place as in Scenarios 2 and 3. However,
prior to running the simulation for 100,000 time steps, the entire
subassemblage at the developed site (patches 1–10 and 170–179) was
translocated to the offset receiving site (patches 81–100) (Figure 1d).
This represented active restoration, where human interventions as-
sisted the reassembly of a damaged ecosystem through reintroduc-
tion of appropriate species (Suding, 2011). In practice, translocations
reintroduce specific species after creating new habitats—such as
newts (Edgar, Griffiths, & Foster, 2005) or frogs (Pickett et al., 2013)
to newly created wetlands—but our simulation took this concept
to its logical extreme by transplanting the whole intact community
from the development site to the offset site. Although perfect trans-
location is practically unrealistic, it allowed us to explore outcomes
when diversity at the start of the simulation was identical to that of
the counterfactual (Scenario 1), albeit with an altered landscape
configuration. After translocation, the birth–death process was run
for 100,000 time steps and the same five diversity patterns were
recorded at the same intervals as the other scenarios.

2.6 | Evaluating simulation outcomes

At the end of the simulation, the outcomes for the 100 iterations
were averaged for each of the five biodiversity patterns. We then
determined the degree to which no net loss was achieved by calcu-
lating the log response ratio of each offset scenario (Scenarios 2–4)
compared to the counterfactual across the duration of the simulation
(Scenario 1). Thus, no net loss was assessed relative to a dynamic ref-
ereence scenario that excluded development, which was necessary
to isolate whether the offset intervention could compensate for the
losses from development to achieve no net loss (Maron et al., 2018;
Maron, Rhodes, & Gibbons, 2013). The log response ratio is the nat-
ural logarithm of the biodiversity patterns for Scenarios 2–4 divided
by the pattern from the counterfactual, Scenario 1. This insured that
all the biodiversity patterns could be represented in the same units.
Here, a log response ratio of zero illustrated no net loss of biodiver-
sity, whereas positive and negative values would represent net gain
and net loss, respectively.

We applied model-based recursive partitioning (Zeileis, Hothorn, &
Hornik, 2008; mob function in party package) to split the log response
ratios into a hierarchical tree comparing the effects of speciation, dis-
persal and offset implementation. Model-based recursive partitioning
is similar to conventional regression trees, but differs in that the termi-
nal nodes of the tree are represented by a parametric regression model.
We regressed the response ratio of each diversity pattern against the
simulation duration (i.e., number of time steps) using a quadratic linear
model. Although regression is not ideal for analysing time series data,
we deemed it appropriate here because the aim was not to estimate
model parameters, but rather to test the effects of regressor vari-
ables (speciation, dispersal or management scenario). As such, a sim-
pler regression was favoured over more complex time series analysis.
Similarly, we preferred a quadratic linear regression over more intricate
generalized linear modes because it provided an accurate, yet flexible,
representation of the varying functional forms for the different diver-
sity trajectories (as illustrated by the adjusted-\( R^2 \) values in Figures 2–4).
Model-based recursive partitioning works by regressing the log response ratios of the diversity patterns against the simulation duration and then incrementally adding regressor variables (speciation and dispersal as continuous regressor variables and type of offset scenario as a categorical regressor). If the addition of a regressor variable reduced the stability of the model (measured as the difference in model deviance) then the tree was split along the least stable variable and the process was repeated for the other branches of the tree. Thus, splits at the root of the tree represented regressor variables with the greatest influence on simulation outcomes. To prevent overfitting, we pruned the tree by limiting the number of data points at each terminal node of the tree to a minimum of 350.

3 | RESULTS

Initializing the neutral simulation resulted in predictable patterns for combinations of speciation and dispersal. Both local (Figure S1) and regional species richness (Figure S2) increased with speciation rates, but only the former also increased with dispersal rates. Local species evenness was highest when both speciation and dispersal rates were high (i.e., there were many species able to colonize widely: Figure S3). Regional species evenness, on the other hand, was highest at low speciation and dispersal rates (Figure S4). Predictably, community dissimilarity was highest when speciation rates were high and dispersal rates low, as this combination would result in high levels of narrow-range endemics (Figure S5).

3.1 | Translocation outperformed passive restoration

After running for 100,000 time steps, hierarchical partitioning showed how the choice of offset implementation was the greatest determinant of outcomes (i.e., the first split in the hierarchical tree) for all metrics of biodiversity other than community dissimilarity at both local and regional scales (Figures 2-4). Outcomes for passive restoration (Scenario 3) were only statistically distinguishable from not having any offsets at all (Scenario 2) at regional scales when speciation rates were high (p < 0.0025; Figures 2b and 3b). This indicated that passive restoration offsets would only have a noticeable effect for ecosystems with high starting levels of biodiversity (large regional species pools). In the simulations, translocation (Scenario 4) was the only form of offset that consistently resulted in no net loss or even net gain of biodiversity, regardless
FIGURE 3 Hierarchical regression tree for offset outcomes for (a) local and (b) regional species evenness, partitioned based on management scenario (i.e., no offsets, passive restoration and translocation), speciation and dispersal rates. Partitions at the root of the tree represent more influential regressor variable than partitions near the tips of the tree. Plots at the tips of the tree represent biodiversity relative to a dynamic counterfactual of no development for the duration of the simulation, with red lines as the modelled trajectory and horizontal dashed lines as no net loss relative to the counterfactual. Positive and negative response ratios represent net gain and net loss, respectively.

FIGURE 4 Hierarchical regression tree for offset outcomes for community dissimilarity, partitioned based on management scenario (i.e., no offsets, passive restoration and translocation), speciation and dispersal rates. Partitions at the root of the tree represent more influential regressor variable than partitions near the tips of the tree. Plots at the tips of the tree represent biodiversity relative to a dynamic counterfactual of no development for the duration of the simulation, with red lines as the modelled trajectory and horizontal dashed lines as no net loss relative to the counterfactual. Positive and negative response ratios represent net gain and net loss, respectively.
of the metric used (i.e., the response ratio was near or above 0: Figures 2–4).

3.2 | Speciation affects offset outcomes more than dispersal

Speciation rates—and, thus, starting levels of biodiversity—affected offset outcomes for all patterns of biodiversity. However, these were generally small quantitative effects, rather than considerable changes to the general shape of resulting biodiversity trajectories. The effect of speciation on community similarity was more pronounced because species-poor landscapes with low speciation rates \( (\nu < 0.0025) \) became more patchy after development (i.e., community dissimilarity increased; Figure 4). By contrast, dispersal rates only influenced offset outcomes for translocation offsets (Scenario 4), but only for regional-scale patterns of richness and evenness (Figures 2b and 3b).

3.3 | Offset outcomes depend on choice of biodiversity metrics

Speciation, dispersal and the choice of offset implementation combined in similar ways, but had opposing effects depending on the choice of biodiversity metric. At the landscape scale, for instance, recursive partitioning for species richness (Figure 2b) and evenness (Figure 3b) resulted in identical hierarchical trees, but these two metrics showed opposite trajectories: increasing and decreasing, respectively. In this specific example, the initial loss of species could be compensated for through time at the landscape scale, but this resulted in a few abundant species becoming increasingly dominant. Such nuanced changes to biodiversity blur the distinction between overall net loss and net gain.

4 | DISCUSSION

Biodiversity offsetting uptake, technique and legislation has proliferated rapidly. However, unless these approaches consider how ecological and evolutionary complexity influences offset outcomes, they risk oversimplifying biological reality, misdirecting conservation actions and overstating conservation progress (Pressey et al., 2017; Spash, 2015; Turnhout, Waterton, Neves, & Buizer, 2014). It is not enough that biodiversity offsets have a very efficient set of best practice, they also need to be effective at actually mitigating the loss of biodiversity.

In this study, we used neutral theory to compare whether underlying ecological and evolutionary processes affect different forms of offset implementation. Although our simulation contained considerably more biological realism than previous offset models (Bull et al., 2014, 2015; Gibbons et al., 2015; Laitila et al., 2014), it was still based on a very simple synthetic landscape filled with biologically equivalent—and therefore interchangeable—organisms. Despite this simplicity, effective mitigation (i.e., no net loss of biodiversity) was only achieved consistently by translocating organisms from the development site to the offset receiving site. No net loss was hard to achieve for simple synthetic landscapes, which implies that it will be even less likely in the complex ecosystems of the real world.

Encouragingly, our results suggest that more robust offset implementation leads to better mitigation outcomes, regardless of the underlying ecological and evolutionary processes. Therefore, offset policies should insist on active restoration efforts such as translocation, rather than simply restoring habitat capacity to support secondary colonization from the surroundings. Even though restoration is more effective for mobile organisms (e.g., birds recover faster in restored forests than amphibians: Crouzeilles et al., 2016), our neutral simulations illustrated that relying on immigration from the remaining intact habitat could not compensate for biodiversity losses. This was true even when dispersal rates were exceptionally high \( (m = 0.75) \) meant that on average three out of every four organisms immigrated from elsewhere.

The failure of passive restoration in Scenario 3 is concerning because in practice most restoration modifies the physical environment and then manipulates vegetation composition and structure (Hobbs & Harris, 2001; Ruiz-Jaen & Aide, 2005) and higher trophic levels and ecosystem functions are expected to recover naturally thereafter (Suding, 2011). Restoration improves ecosystems from their degraded states, but it rarely restores habitats to the same conditions as intact reference sites (Crouzeilles et al., 2016; Rey Benayas et al., 2009; Suding, 2011). Therefore, biodiversity offsets that rely on imperfect restoration will generally result in a net loss of biodiversity if areas of primary habitat are lost (Curran, Hellweg, & Beck, 2014; Gibbons & Lindenmayer, 2007; Maron et al., 2012).

However, rather than bemoaning how offsets are restricted by the limits of restoration, stringent no net loss policies could instead become a driver for higher standards in restoration and translocation. Currently, 41% of restoration practitioners in Australia cited biodiversity offsetting as a general motivator for initiating ecological restoration (Haggar, Dwyer, & Wilson, 2017) and mitigation-motivated translocations are estimated to be more prevalent than conservation-based releases (Germano et al., 2015). Moreover, offsetting makes developers who cause biodiversity loss responsible for its enhancement somewhere else, which is a more just way of overcoming existing financial and social constraints to effective restoration (Miller & Hobbs, 2007). This emphasizes the influence that offset policies already have on defining the scope and potential of restoration and translocation. Combined with the results from our simulation, this suggests that the need for effective mitigation could—and should—become a catalyst for better ecological restoration.

Bull et al. (2016) called on practitioners to avoid using the hold-all term “biodiversity” and specify exactly which components of biodiversity they aim to offset. While this sensible recommendation reduces ambiguity, it offers no scientific way of clarifying which measures of biodiversity are most appropriate (Ives & Bekesy, 2015). Among published biodiversity offset studies, the most frequently used metrics of biodiversity are those for ecosystem structure (e.g.,
Although neutral theory is still a simplification of the real world, it provides more biological realism than earlier biodiversity offset models. Our study showed that although ecological and evolutionary processes do affect biodiversity offset outcomes, these effects are secondary to the way offsets are implemented. This is encouraging because it implies that biodiversity offsets can be successful across all the continents and biogeographical realms in which they are being planned (Maron et al., 2016). Ultimately, however, our findings illustrate how success hinges on effective restoration. This emphasizes the need for mitigation policies and guidelines that demand the highest standards of active restoration and translocation.

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CONFLICT OF INTEREST

None.

DATA ACCESSIBILITY

The R-scripts to recreate these simulations are available on Dryad (https://doi.org/10.5061/dryad.nn9410n).

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REFERENCES

Anderson, M. J., Ellingsen, K. E., & McArdle, B. H. (2006). Multivariate dispersion as a measure of beta diversity. Ecology Letters, 9, 683–693. https://doi.org/10.1111/j.1461-0248.2006.00926.x
Bezombes, L., Kerbiriou, C., & Spiegelberger, T. (2019). Do biodiversity offsets achieve No Net Loss? An evaluation of offsets in a French department. Biological Conservation, 231, 24–29. https://doi.org/10.1016/j.biocon.2019.01.004
Bull, J. W., Gordon, A., Law, E. A., Suttle, K. B., & Milner-Gulland, E. J. (2013). Biodiversity offsets in theory and practice. Conservation Biology, 28, 799–809. https://doi.org/10.1111/cobi.12243
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, 1686–1693. https://doi.org/10.1111/1365-2664.12726
Bull, J. W., Hardy, M. J., Moilanen, A., & Gordon, A. (2015). Categories of flexibility in biodiversity offsetting, and their implications for conservation. Biological Conservation, 192, 522–537. https://doi.org/10.1016/j.biocon.2015.08.003
Bull, J. W., & Strange, N. (2018). The global extent of biodiversity offset implementation under no net loss policies. Nature Sustainability, 1, 790–798. https://doi.org/10.1038/s41893-018-0176-z
Bull, J. W., Suttle, K. B., Gordon, A., Singh, N. J., & Milner-Gulland, E. J. (2013). Biodiversity offsets in theory and practice. Oryx, 47, 369–380. https://doi.org/10.1017/S003060531200172X

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habitat area) and population size (e.g., vegetation per cent cover or number of trees per unit area) (Gonçalves, Marques, Soares, & Pereira, 2015). These metrics are generally easier to measure than metrics of community composition, species traits or ecological processes and functions. However, our simulation demonstrated clearly that offset outcomes depended on the choice of biodiversity metric. For example, species richness in Scenarios 2 and 3 gradually converged towards the counterfactual (Figure 2) supporting the general impression that biodiversity recovers more completely after more time has passed since restoration (e.g., Crouzeilles et al., 2016). However, in the same simulations, species evenness diverged from the same counterfactual through time (Figure 3); illustrating that the community was becoming dominated by a few hyper-abundant species.

Since community evenness is important for maintaining ecological functioning during periods of environmental stress (Wittebolle et al., 2009), ignoring it in offset projects could reduce the resilience of ecosystems. Therefore, mitigation would be improved by monitoring more than one biodiversity metric (such as different combinations of essential biodiversity variables: Pereira et al., 2013; Gonçalves et al., 2015) and conceding that mitigation will never be a simple equation of gains versus losses, but rather a continuous trade-off between different aspects of biodiversity. Ultimately, the imprecise definition of biodiversity means that biodiversity exchanges are strictly not commensurable and, therefore, no different from bartering; albeit sophisticated bartering (Spash, 2015; Walker et al., 2009).

This more complex view also reiterates that biodiversity is not just a collection of plants and animals that can be exchanged, but rather the legacy of historical speciation. Therefore, a central goal of biodiversity offsetting must be to avoid the erosion of evolutionary potential (Moreno-Mateos et al., 2015). Unlike earlier offset models, neutral theory simulated speciation explicitly and showed that biodiversity offsets can be used successfully under different speciation rates. This does not imply that speciation will affect mitigation outcomes post-offsetting. Instead this finding should be interpreted that offsets can theoretically be successful across various taxa and geographic localities that differ in historical diversification rates; assuming, of course, that offsets are implemented effectively.

While neutral theory is useful for evaluating offset outcomes after incorporating ecological and evolutionary processes, it too has limitations. For one, the assumption of equivalent fitness of individuals is unlikely to hold for real organisms (Clark, 2012). In this regard, neutral theory overestimates the availability of like-for-like exchanges of biodiversity and, therefore, the likelihood of a successful offset outcome (Pilgrim et al., 2013; Quétier & Lavorel, 2011). Moreover, the simulated landscape ignored trophic interactions and species dependencies, suggesting that this study represents the best-case scenario when evaluating the exchangeability of biodiversity across different localities. Although adding niche-based community assembly rules to our simulations is possible, this would probably make it even more difficult to achieve no net loss.
Burgin, S. (2008). BioBanking: An environmental scientist’s view of the role of biodiversity banking offsets in conservation. Biodiversity and Conservation, 17, 807–816. https://doi.org/10.1007/s10531-008-9319-2

Buschke, F. T., Brendonck, L., & Vanschoenwinkel, B. (2016). Adding energy gradients and long-distance dispersal to a neutral model improves predictions of Madagascar bird diversity. Ecology and Evolution, 6, 6919–6929. https://doi.org/10.1002/ece3.2379

Clark, J. S. (2012). The coherence problem with the unified neutral theory of biodiversity. Trends in Ecology and Evolution, 27, 198–202. https://doi.org/10.1016/j.tree.2012.02.001

Crouzeilles, R., Curran, M., Ferreira, M. S., Lindenmayer, D. B., Grelle, C. E. V., & Rey Benayas, J. M. (2016). A global meta-analysis on the ecological drivers of forest restoration success. Nature Communication, 7, 11666. https://doi.org/10.1038/ncomms11666

Curran, M., Hellweg, S., & Beck, J. (2014). Is there any empirical support for biodiversity offset policy? Ecological Applications, 24, 617–632. https://doi.org/10.1890/13-0243.1

Edgar, P. W., Griffiths, R. A., & Foster, J. P. (2005). Evaluation of translocations as a tool for mitigating development threats to great crested newts (Triturus cristatus) in England, 1990–2001. Biological Conservation, 122, 45–52.

Etienne, R. S. (2005). A new sampling formula for neutral biodiversity. Ecology Letters, 8, 253–260. https://doi.org/10.1111/j.1461-0248.2004.00717.x

Etienne, R. S., Latimer, A. M., Silander, J. A. J., & Cowling, R. M. (2006). Comment on “Neutral ecological theory reveals isolation and rapid speciation in a biodiversity hot spot”. Science, 311, 610b–610b. https://doi.org/10.1126/science.1121914

Gernan, J. M., Field, K. J., Griffiths, R. A., Clulow, S., Foster, J., Harding, G., & Swaisgood, R. R. (2015). Migration-driven translocations: Are we moving wildlife in the right direction? Frontiers in Ecology and Evolution, 3, 100–105. https://doi.org/10.1890/140137

Gibbons, P., Evans, M. C., Maron, M., le Gordon, A., von Roux, D., Hase, A., ... Possingham, H. P. (2015). A loss-gain calculator for biodiversity offsets and the circumstances in which no net loss is feasible. Conservation Letters, 9, 252–259. https://doi.org/10.1111/conl.12206

Gibbons, P., & Lindenmayer, D. B. (2007). Offsets for land clearing; no net loss or the tail wagging the dog? Ecological Management and Restoration, 8, 26–31. https://doi.org/10.1111/j.1442-8903.2007.00328.x

Gibbons, P., Macintosh, A., Constable, A. L., & Hayashi, K. (2018). Outcomes from 10 years of biodiversity offsetting. Global Change Biology, 24, e643–e654.

Gómez-Aparicio, L. (2009). The role of plant interactions in the restoration of degraded ecosystems: A meta-analysis across life-forms and ecosystems. Journal of Ecology, 97, 1202–1214. https://doi.org/10.1111/j.1365-2745.2009.01573.x

Gonçalves, B., Marques, A., Soares, A. M. V. D. M., & Pereira, H. M. (2015). Biodiversity offsets: From current challenges to harmonized metrics. Current Opinion in Environmental Sustainability, 14, 61–67. https://doi.org/10.1016/j.cosust.2015.03.008

Hagger, V., Dwyer, J., & Wilson, K. (2017). What motivates ecological restoration? Restoration Ecology, 25, 832–843. https://doi.org/10.1111/rec.12503

Harpole, W. S., & Tilman, D. (2006). Non-neutral patterns of species abundance in grassland communities. Ecology Letters, 9, 15–23.

Hobbs, R. J., & Harris, J. A. (2001). Restoration ecology: Repairing the earth’s ecosystems in the new millennium. Restoration Ecology, 9, 239–246. https://doi.org/10.1111/j.1526-100X.2001.00900239.x

Holt, B. G., Lessard, J., Borregaard, M. K., Fritz, S. A., Araújo, M. B., Dimitov, D., ... Rahbek, c. (2013). An update of Wallace’s zoogeographic regions of the world. Science, 339, 74–78. https://doi.org/10.1126/science.1228282

Hubbell, S. P. (2001). The unified neutral theory of biodiversity and biogeography. Princeton, NJ: Princeton University Press.
Munoz, F., & Huneman, P. (2016). From the neutral theory to a comprehensive and multiscale of ecological equivalence. The Quarterly Review of Biology, 91, 321–342.

Nathan, R., & Muller-Landau, H. C. (2000). Spatial patterns of seed dispersal, their determinants and consequences for recruitment. Trends in Ecology and Evolution, 15, 278–285. https://doi.org/10.1016/S0169-5347(00)1874-7

Noss, R. F. (1990). Indicators for monitoring biodiversity: A hierarchical approach. Conservation Biology, 4, 355–364. https://doi.org/10.1111/j.1523-1739.1990.tb00309.x

Pereira, H. M., Ferrier, S., Walters, M., Geller, G. N., Jongman, R. H. G., Scholes, R. J., BruFord, M. W., Brummitt, N., Butchart, S. H. M., Cardoso, A. C., Coops, N. C., Dulloo, E., Faith, D. P., Freyhof, J., Gregory, R. D., Heip, C., Höft, R., Hurrut, G., Jetz, W., Karp, D. S., McGeoch, M. A., Obura, D., Onoda, Y., Pettorelli, N., Reyers, B., Sayre, R., Scharlemann, J. P. W., Stuart, S. N., Turak, E., Walpole, M., & Wegmann, M. (2013). Essential biodiversity variable. Science, 339, 277–278. https://doi.org/10.1126/science.1229931

Pickett, E. J., Stockwell, M. P., Bower, D. S., Garnham, J. I., Pollard, C. J., Clulow, J., & Mahony, M. J. (2013). Achieving no net loss in habitat offset of a threatened frog required high offset ratio and intensive monitoring. Biological Conservation, 157, 156–162. https://doi.org/10.1016/j.biocon.2012.09.014

Pieiou, E. C. (1966). The measurement of diversity in different types of biological collections. Journal of Theoretical Biology, 13, 131–144. https://doi.org/10.1016/0022-5193(66)90013-0

Pilgrim, J. D., Brownlie, S., Ekstrom, J. M. M., Gardner, T. A., von Hase, A., ten Kate, K., ... ward, G. (2013). A process for assessing the offsetability of biodiversity impacts. Conservation Letters, 6, 376–384. https://doi.org/10.1111/conl.12002

Pressey, R. L., Weeks, R., & Gurney, G. G. (2017). From displacement activities to evidence-informed decisions in conservation. Biological Conservation, 212, 337–348.

Quétier, F., & Lavorel, S. (2011). Assessing ecological equivalence in biodiversity offset schemes: Key issues and solutions. Biological Conservation, 144, 2991–2999. https://doi.org/10.1016/j.biocon.2011.09.002

R Core Team (2016). R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing. Retrieved from https://www.R-project.org

Rangel, T. F. L. V. B., & Diniz-Filho, J. A. F. (2005). Neutral community dynamics, the mid-domain effects and spatial patterns in species richness. Ecology Letters, 8, 783–790.

Rey Benayas, J. M., Newton, A. C., Diaz, A., & Bullock, J. M. (2009). Enhancement of biodiversity and ecosystem services by ecological restoration: A meta-analysis. Science, 325, 1121–1124. https://doi.org/10.1126/science.1172460

Rosindell, J., Hubbell, S. P., & Etienne, R. S. (2011). The unified neutral theory of biodiversity and biogeography at age ten. Trends in Ecology and Evolution, 26, 340–348. https://doi.org/10.1016/j.tree.2011.03.024

Rosindell, J., Wong, Y., & Etienne, R. S. (2008). A coalescence approach to spatial neutral theory. Ecological Informatics, 3, 259–271.

Ruiz-Jaen, M. C., & Aide, T. M. (2005). Restoration success: How is it being measured? Restoration Ecology, 13, 569–577. https://doi.org/10.1111/j.1526-100X.2005.00072.x

Spash, C. L. (2015). Bulldozing biodiversity: The economics of offsets and trading-in nature. Biological Conservation, 192, 541–551. https://doi.org/10.1016/j.biocon.2015.07.037

Suding, K. N. (2011). Toward an era of restoration in ecology: Successes, failures, and opportunities ahead. Annual Review of Ecology, Evolution and Systematics, 42, 465–487. https://doi.org/10.1146/annurev-ecolsys-102710-145115

Tuomisto, H., Ruokolainen, K., & Yli-Halla, M. (2003). Dispersal, environmental and floristic variation of western Amazonian forests. Science, 299, 241–244. https://doi.org/10.1126/science.1078037

Turnhout, E., Waterton, C., Neves, K., & Buizer, M. (2014). Technocratic and economic ideals in the ecosystem services discourse. Conservation Letters, 7, 336–337. https://doi.org/10.1111/conl.12069

Walker, S., Brower, A. L., Stephens, R. T. T., & Lee, W. G. (2009). Why bartering biodiversity fails. Conservation Letters, 2, 149–157. https://doi.org/10.1111/j.1755-263X.2009.00061.x

Wittebolle, L., Marzorati, M., Clement, L., Ballo, A., Daffonchio, D., Heylen, K., ... Boon, N. (2009). Initial community evenness favours functionality under selective stress. Nature, 458, 623–626. https://doi.org/10.1038/nature07840

Zaloumis, N. P., & Bond, W. J. (2011). Grassland restoration after afforestation: No direction home? Austral Ecology, 36, 357–366. https://doi.org/10.1111/j.1442-9933.2010.02158.x

Zeileis, A., Hothorn, T., & Hornik, K. (2008). Model-based recursive partitioning. Journal of Computational and Graphical Statistics, 17, 492–514. https://doi.org/10.1198/106186008X319331

BIOSKETCHES

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Author contributions: FB designed the simulation framework and analysed the outputs. Both authors wrote the manuscript.

SUPPORTING INFORMATION

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

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