Title: Neighborhood habitat gains increase plant species richness in forest fragments

Short Running Title: Neighborhood habitat increases richness

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Abstract

Theory and indirect evidence suggest that when new habitat is added to a habitat fragment's local landscape, or "neighborhood", species richness in the fragment will increase. Although this hypothesis is frequently assumed, it has not yet been tested directly with longitudinal data. In a natural forest regeneration experiment on Aotearoa New Zealand's South Island, we use causal inference to show that 41-year changes in fragment-scale understory plant species richness are driven by changes in neighborhood habitat over the past century. This result supports theoretical predictions and highlights avenues for further research. Our findings can help inform prioritization of habitat restoration and conservation efforts.

Introduction

Habitat loss is changing the spatial distribution of biodiversity worldwide and is a major driver of global biodiversity loss (Haddad et al. 2015, Watson et al. 2018, Chase et al. 2020). Consequently, it is imperative to identify mechanisms that can boost the diversity of locally indigenous habitat specialist species in remaining habitat fragments.

One approach thought to increase species richness in habitat fragments is restoration of habitat in the surrounding landscape. Most theories of habitat loss and fragmentation predict that fragments with more habitat in their "neighborhoods" will contain more habitat specialist species (MacArthur & Wilson 1963, Haila 2002, Fahrig 2013). Empirical studies confirm this prediction (Torrenta & Villard 2017, Watling et al. 2020). A temporally explicit extension of this hypothesis suggests that when new habitat is added to a fragment's neighborhood, species richness in the fragment will increase. We refer to this expectation as the "Habitat Gain Hypothesis".

To our knowledge, the Habitat Gain Hypothesis—while often discussed (Farneda et al. 2015, García-Martínez et al. 2017, Newmark et al. 2023)—has not been tested directly with longitudinal data. Long-term studies in fragmented landscapes have supported the inverse hypothesis—i.e., that species are lost following neighborhood habitat loss (Ferraz et al. 2007, Horváth et al. 2019). However, changes in ecological systems are not always straightforwardly reversible (Holling 1973, Pardini et al. 2010), and it is unclear to what extent, or how quickly, restored habitat can substitute for habitat previously lost (Whytock et al. 2018). A direct, long-term test of the Habitat Gain Hypothesis would provide valuable new evidence to help guide management decisions in fragmented landscapes.

Testing the Habitat Gain Hypothesis poses challenges because the relevant ecological processes can be too slow for a typical field study. When a landscape loses habitat, e.g., forest or wetland, it takes decades of active or passive restoration for lost habitat to be regained and ecosystem functioning restored (Suding 2011, Meli et al. 2017). Compounding the timescale problem, biotic responses to changing habitat cover often lag behind the habitat changes (Lira et al. 2019, Watts et al. 2020). Thus, detecting species richness responses to large-scale habitat gains requires data on both species richness and habitat cover spanning decades or more. Conventional ecological methods rarely provide such spatiotemporally extensive datasets. Instead, it may be necessary to take a historical ecology approach, whereby unconventional sources are used to glean ecological data from times and places that are not represented in conventional data sets (Vellend et al. 2013). Historical ecology methods often rely on resources like historical maps and legacy studies, in which biodiversity data were recorded at unmarked locations that cannot be resurveyed with strong spatial precision. Despite the challenges associated with these data sources, they provide unique insights into ecosystems' historical states.

Here, we use causal inference tools to test the Habitat Gain Hypothesis for forest-specialist understory vascular plants in 26 forest fragment reserves using a natural experiment of forest regeneration in the deforested landscape of Banks Peninsula, South Island, Aotearoa New Zealand (Fig. 1). We quantify 41-year changes in reserve-scale species richness by repeating a historical vegetation survey, and we test whether proportional changes in species richness are driven by century-scale changes in neighborhood forest cover. We also use the data to generate preliminary estimates of reserve-scale immigration and extinction rates, which help elucidate the demographic processes underlying the effects of neighborhood habitat gains.

Materials & Methods

Study area

Before anthropogenic deforestation began on Banks Peninsula-Te Pātaka o Rākaihautū several centuries ago, this roughly 1,300 km^2 landscape was covered by nearly continuous evergreen forest (Wilson 2013). Following Māori arrival, some portion of this forest was burned in Māori cultural practices, and more was cleared subsequently by European colonists for pasture and wood products (Ogilvie 2007, Wilson 2013). By approximately 1920, less than 1% of original forest cover remained in isolated fragments, surrounded by a matrix of primarily non-indigenous grass and forb-dominated pasture with small areas of regenerating forest (Wilson 2013). Since then, a combination of passive and active forest restoration has increased indigenous forest cover across the landscape, with second-growth patches regenerating in the local neighborhoods around our 26 focal sites, which have historically been designated "Scenic Reserves" and thereby protected from deforestation (Wilson 2013). These reserves range in area from 0.06-45.58 ha, elevation from 20 to 765 m, mean annual temperature from 8.3 to 12.2 °C (Karger et al. 2017, Karger et al. 2018), and mean annual precipitation from 626-1,215 mm (Karger et al. 2017, Karger et al. 2018). Soil conditions are heterogeneous across Banks Peninsula, a spatially complicated mix of mostly moderately fertile soils based on volcanic rock overlayed to varying degrees with loess from wind-blown silt from weathered sedimentary rocks of the Southern Alps (Wilson 2013).

Focal taxa

We focus on understory plants (herbs, shrubs, and climbers) because their short life cycles can help minimize lags in response to habitat change (Lira et al. 2019). Prior work has shown that long-lived taxa like trees are more likely to exhibit extinction lags following habitat loss (Lira et al. 2019). Because many of our sites have remained forested for centuries or more, we hypothesized that our sites may not yet have lost many, if any, longer-lived species through "relaxation" following habitat loss in their surrounding neighborhoods (Diamond 1972, Loehle 2018). In contrast, we hypothesized that short-lived species would already have had sufficient time to undergo "relaxation" in response to historical habitat loss, and thus there would be more opportunity for short-lived taxa to re-immigrate. Our analysis is restricted to obligate forest taxa because data for these taxa are comparable between time points (see below).

Baseline survey

To quantify species richness in 1970 for the 26 forest fragment reserves, we used data from Kelly (1972). Kelly (1972) surveyed each reserve using transect routes of varying lengths, which cover each habitat type (including both forest and non-forest) identified a priori from aerial photos. The lengths of routes were apportioned among habitat types in approximate proportion with their percent cover within the reserve. For example, if a given habitat type covered approximately 20% of a reserve, then approximately 20% of total survey route for that reserve was assigned to that habitat type. The exact routes (not documented) were designed haphazardly or pseudo-randomly, but independently of ease of access (G. Kelly pers. comm.). All indigenous vascular plant species observed were recorded. Survey effort was quantified by the total number of hours spent surveying each reserve.

Kelly (1972) also documented whether each reserve was enclosed by a livestock exclusion fence. A map, showing habitat type delineations, was drawn for each reserve using aerial photos and field observations.

Kelly (1972) recorded soil fertility on an ordinal scale with five categories: “low”, “low-medium”, “medium”, “high-medium”, and “high”. We collapsed these data into two categories, one for “low” through “medium”, and the other for “high-medium” and “high”.

Repeat survey

To quantify reserve-scale species richness in 2011, we repeated a modified version of Kelly’s (1972) survey. In each reserve, we surveyed 4–15 50 m transects apportioned among forest types, classified by dominant tree species, in approximate proportion with their percent cover within the reserve in 2011. (Three reserves were too small for 50 m transects, so 10 m transects were used instead.) The issue of accounting for sampling effort in data analysis is discussed below in the section on statistical analyses. We recorded all indigenous vascular plant species observed within 2 m of each transect. Within patches of each forest type, transects were placed randomly, yielding a stratified random sampling design. The total number of transects for each reserve was set in approximate proportion to the total area of forest in that reserve. We quantified 2011 survey effort using the total length of transects surveyed at each reserve.

Although some reserves include non-forest habitats, we surveyed forest only because we aimed to quantify biotic responses to forest cover changes. Because Kelly’s (1972) survey data also included non-forest habitat, we filtered both data sets to obligate forest taxa to make them comparable. Of the 340 taxa recorded in 1970 and 2011 combined, 45 were forest-specialists and 288 non-specialist, and 7 taxa that were observed but not identified to species level were designated as uncertain. We derived habitat use designations for 243 species from Wilson (2013). For taxa not discussed in Wilson (2013), we used the Flora of New Zealand (Allan 1961, Moore & Edgar 1970, Edgar & Connor 2000) wherever possible (88 taxa), and for the remaining 9 taxa, we searched the peer-reviewed literature (Wiser 2001, Chambers & Farrant 1998, Glenny & Cruickshank 2011, Thorsen et al. 2011, Partridge 1989, Brownsey & Chinnock 1984, Perrie et al. 2010). Habitat designations and references for all species observed are given in Supplementary Table S1.

While all occurrence records were identified at least to genus level, 6% of taxon-by-site occurrences were not identifiable at the species level. For each of these occurrences, we used voucher specimens and photos to define the set of possible species identities. We then generated 100 versions of the data set, in which each uncertain taxon-by-site occurrence is assigned randomly to one of its possible species identities. We then used these 100 simulated data sets to compute the mean species richness at each site for each time point. These values represent the central tendency of the uncertainty in species richness defined by the unidentified taxon-by-site occurrences.

Quantifying neighborhood habitat

We quantified neighborhood habitat change in a way that aims to account for possible lagged effects of habitat changes on species richness (Lira et al. 2019). Rather than using habitat cover in 1970 as our baseline measurement, we instead used a historical map depicting habitat cover in 1920. To quantify neighborhood habitat gains between 1920 and 2012, we compared a historical map of Banks Peninsula forest cover in 1920 (Wilson 2013) against 2012 data from the New Zealand Landcover Database version 5.0 (LCDB v5.0 2018). This period in Banks Peninsula history was of gradual increase in forest cover largely through natural regeneration (Ogilvie 2007, Wilson 2013). The following LCDB categories were included as forest: “Manuka and/or kanuka”, “Broadleaved indigenous hardwoods”, and “Indigenous forest”. We excluded *Pinus* plantations because these areas contain few indigenous forest plants as they are clear-felled on a 25–30-year rotation. We assume that the one-year gap between our 2011 survey and the 2012 habitat data had negligible influence on our analysis.

The 1920 forest map, as well as Kelly’s (1972) reserve maps from 1970, were georeferenced in QGIS version 3.18.2 (qgis.org 2022). Areas designated as old-growth forest by Kelly (1972) were visually compared against old growth fragments from Wilson’s (2013) map in QGIS. The amount and coarse-scale configuration of old-growth forest inside reserves is approximately equal between the two data sources, but there are differences in the placement of some individual fragments up to several hundred meters. We concluded that the 1920 forest cover data are not precise enough for reliable incidence function metrics of habitat connectivity (Prugh 2009), in which small discrepancies in patch locations can influence connectivity values substantially. Instead, we opted for the simpler buffer metric (Prugh 2009, Watling et al. 2020), in which total habitat area is summed within a given radius from the focal site. We generated seven versions of this variable using radii of 0.1 km, 0.2 km, 0.5 km, 1 km, 2 km, 3 km, and 6 km. The radii from 0.2 km through 6 km were chosen following Watling et al. (2020). The 0.1 km radius was added because 0.2 km was favored in many cases (see Results), and we wanted to determine whether smaller radii might perform better. We did not include longer radii because the mean distance between sites was only 16 km, and the longest radii in Watling et al.’s (2020) set did not perform well.

Other covariates

In our statistical models, we included an “adjustment set” of five additional covariates (listed below), which were selected to block all possible confounding paths between neighborhood habitat gains and species richness changes (Pearl 2009, McElreath 2020, Arif & MacNeil 2023). Confounding occurs when the true causal effect of one variable on the other is obscured by the effect of a third variable, or multiple other variables. For example, if two species have weak competitive effects on each other, but temperature has a strong positive effect on both species, then a naïve analysis of the species' occurrence probabilities might suggest that one species facilitates the other. In this example, temperature is a confounder, and including it as a covariate in a regression can remove its confounding influence, provided an appropriate functional form is chosen to link the variables in the statistical model, e.g., linear, exponential, etc. For our analysis, we used a directed acyclic graph (DAG), shown in Fig. 2, to outline a priori assumptions regarding how variables might affect each other. This DAG allows us to identify "back-door" causal pathways that could cause confounding between our cause and effect of interest (Pearl 2009, McElreath 2020, Arif & MacNeil 2023).

Using Pearl's (2009) "back door criterion", we identified an "adjustment set" of five covariates that block all confounding causal paths in Fig. 2. These variables are reserve forest area, presence-absence of a fence designed to exclude mammalian sheep and cattle, presence-absence of walking tracks, soil fertility, and a variable quantifying relative survey completeness for 2011 versus 1970. By including these variables as covariates alongside the neighborhood habitat gain predictor, we can obtain an unbiased estimate of the effect of neighborhood habitat gains on percent changes in species richness, provided our baseline assumptions in Fig. 2 are valid. This also assumes that the functional forms in our regression model are appropriate. Different functional forms are explored in the alternative analyses detailed below. Fig. 2 also includes two quantities for which data were not available: neighborhood human activity and reserve understory density. These variables are difficult to accurately quantify and could have affected relevant ecological processes in the study system, but their potential confounding influences are controlled for by the adjustment set we used. Many other variables could affect either our predictor of interest or the response, but we do not consider them here because they are not expected to cause confounding of our target causal estimand. Including other variables without a clear understanding of their place in the causal structure risks creating a "causal salad" problem found in many observational studies (McElreath 2020, Arif & MacNeil 2023).

We used Kelly's (1972) maps, georeferenced in QGIS, to quantify the total area of forest in each reserve, as discussed above. Our fencing and soil fertility data come from Kelly (1972), and our field observations found no changes in fencing status between 1970 and 2011. Data on walking tracks were obtained in the same way and also showed no change in status. To account for differences in survey completeness between 1970 and 2011 for each reserve (de la Sancha & Boyle 2019), we used the total distance of transects surveyed in 2011 divided by the hours of survey effort recorded in 1970. Because some reserves contain non-forest habitats, which Kelly's (1972) survey included, we multiplied Kelly's hours of survey effort at each reserve by the proportion of that reserve which is forested.

A correlation matrix of predictor variables is given in Supplementary Table S2.

Main statistical analysis

We fit our main regression model using OLS via base R's "lm" function. The response variable, which we modeled with a Gaussian distribution, was the percent change in observed species richness at each reserve between 1970 and 2011. Note that percent change is a continuous variable that can range from -1 (or -100%) to infinity. We refer to this quantity as the “index of species richness change”. This variable can be regarded as an indication of relative changes in species richness across reserves, which serves our purpose of testing whether changes in species richness are more positive or less negative when neighborhood habitat gains increase. Even if absolute changes in species richness are not known, this method allows us to ask whether neighborhood habitat gains influence species richness in a positive direction, provided that variation in sampling effort has been controlled for appropriately. In the “Alternative analyses” and “Rarefaction” sections below, we introduce additional methods we used to control for sampling effort in alternative ways. Our index of species richness change uses the percent change in species richness, rather than the raw change, because we regard the conservation significance of a one-species gain or loss as inversely proportional to the baseline species richness. In other words, we regard losing or gaining a species as more important when there are fewer species at baseline.

The six predictors in our regression models are neighborhood habitat changes, reserve forest area, presence-absence of a fence designed to exclude mammalian browsers, presence-absence of walking tracks, soil fertility, and a variable quantifying relative survey completeness for 2011 versus 1970. Our target causal estimand was the effect of neighborhood habitat changes on our index of species richness change. By Pearl’s (2009) back door criterion, this causal estimand can be estimated statistically as the coefficient of the neighborhood habitat change predictor in the regression model described here, assuming we have used appropriate functional forms linking the variables in our statistical model. (A different functional form is explored in one of the alternative analyses described below.) The full model structure is given below. All continuous predictors were z-scaled (mean zero, SD 1).

$$Y_i \; N(\mu_i, \sigma^2)$$
$$\mu_i = \beta_0 + \beta_1 x_{1i} + \beta_2 x_{2i} + \beta_3 x_{3i} + \beta_4 x_{4i} + \beta_5 x_{5i} + \beta_6 x_{6i}$$

Y_i represents the index of species richness change, and $x_{1i} \dots x_{5i}$ represents our six fixed effect predictors, with coefficients $\beta_1 \dots \beta_6$. β_0 represents the intercept.

We used AICc to compare the models built with the seven different buffer radii for neighborhood habitat change variable (0.1 km, 0.2 km, 0.5 km, 1 km, 2 km, 3 km, and 6 km). Whenever the model favored by AICc is favored by 2 or more, we report only results for the favored model. When another model is within 2, we report results for all models inside this cutoff.

Alternative analyses

To examine the robustness of our results, we used three alternative approaches to accounting for sampling effort. First, we aimed to account for the possibility of a different functional form linking the sampling effort ratio to species richness changes. Species richness is often found to vary logarithmically with survey effort, so we refit the main model with the effort ratio log transformed.

In the other two models, instead of including sampling effort ratio as a covariate in the adjustment set, we attempted to remove the influence of sampling effort from the data via rarefaction prior to regression analysis. Details of the rarefaction procedure are given in the next section. In one analysis of the rarefied data, we again used the apparent percent change in species richness (i.e., the index of species richness change) as the response variable. The model structure for this analysis is identical to the main model structure, except the sampling effort ratio covariate is omitted. In the other analysis, we modeled species richness itself as a time series, with each site represented by two observations (one in 1970 and one in 2011). Additionally, instead of using changes in neighborhood habitat as an independent variable, we used the "before" and "after" values of neighborhood habitat amount. The model structure for the rarefied time series model is specified below.

In our time series analysis, we initially modeled species richness as a Gaussian random variable in a linear mixed model. Our data set contained non-integer species richness values due to our method of accounting for specimen identification uncertainty (see above), so the Poisson error distribution commonly used for species richness values was not appropriate here, nor were other discrete distributions. Model checking with the DHARMa R package (Hartig, 2022) indicated that the Gaussian distribution was appropriate. The model structure is given below.

$$Y_{ij}\ N\left(\mu_{ij}, \sigma_Y^2\right)$$
$$\mu_{ij} = \beta_0 + \beta_1 x_{1j} + \beta_2 x_{2ij} + \beta_3 x_{3i} + \beta_4 x_{4i} + \beta_5 x_{5i} + \beta_6 x_{6i} + \beta_7 x_{2ij} x_{3i} + u_i$$
$$u_i\ N(0, \sigma_u^2)$$

Y_{ij} represents species richness at site i and timepoint j. x_{1j} is a binary predictor distinguishing the first and second time points. x_{2ij} represents the neighborhood habitat amount at site i and timepoint j. x_{3i} represents the forest patch size for site i. x_{4i} is a binary variable indicating whether site i is fenced. x_{5i} is a binary variable indicating whether site i contains walking tracks. x_{6i} is a binary variable distinguishing high versus low soil fertility. β_7 is the coefficient on a multiplicative interaction between neighborhood habitat amount and forest patch size, to address the hypothesis that neighborhood habitat may have a smaller effect on reserves that are large on thus contain many species irrespective of spillover effects from nearby patches. β_0 represents the universal intercept term. The target causal estimand is β_2, the effect of neighborhood habitat amount on species richness. We built the model with rarefied species richness data, which are described in the next section.

The time series model specified above yielded significant positive spatial autocorrelation in the residuals. To correct this issue, we rebuilt the model structure described above with two additional terms: cubic regression splines for the geographic "x" and "y" coordinates (in the New Zealand Map Grid system, EPSG27200). We built this model using the R package mgcv. As recommended by Wood (2017), we used the maximum possible basis dimension ("k") for each spline. We allowed mgcv's "leave-one-out" cross validation algorithm to determine the optimal value of lambda, the "wiggliness penalty" that determines the second derivatives of the smooth functions produced by the splines. Refitting this model with splines for x and y yielded no significant residual spatial autocorrelation.

Standard model checking steps for all models are shown in our publicly available R code. The R package DHARMa (Hartig, 2022) was used for checking the generalized linear mixed models.

Rarefaction

Species richness data were rarefied as follows. First, we computed, for each site, the ratio of transects surveyed in 2011 to hours spent surveying in 1970. (These were the best available metrics of sampling effort for each survey.) Because the 2011 data could be rarefied (by omitting transects), whereas the 1970 data could not, we used the site with the least ratio of 2011 transects to 1970 hours as our benchmark for rarefaction. Data for all other sites were then rarefied by subsampling the number of 2011 transects at each site that produces a ratio of transects/hours that most closely matches the benchmark ratio. (Perfect matches were usually not possible because transects can only be counted as integers.) Rarefied 2011 species richness was computed for each site as the mean species richness of 100 randomly sampled subsets of transects. The rarefaction procedure is shown in full in the R code.

Because Kelly's (1972) survey routes were not recorded, it is not possible to ensure that our sampling effort in 2011 was equal to Kelly's. Instead, our rarefaction procedure ensures that the factor by which we over- or under- calibrated our sampling effort, relative to Kelly, is equal across sites. Consequently, as we discuss above, our data are not suitable for drawing conclusions regarding absolute changes in species richness. Rather, our analyses are designed for relative comparison across reserves, so that we can ask whether neighborhood habitat gains influence species richness changes in the positive direction.

Modeling immigration and extinction rates

The two demographic processes underlying reserve-scale species richness changes are immigration and local extinction. We used the rarefied data to explore the contributions of these two processes to overall causal relationship between neighborhood habitat changes and species richness changes. As only two time points were observed, our immigration and extinction rate estimates simply represent the net observed gains and losses of species over the study interval, standardized by initial richness. We refit our main model structure with each rate as a response variable.

As discussed in previous sections, our methods are designed to ensure that the factor by which we over- or under- calibrated our sampling effort, relative to Kelly, is equal across sites. They are not designed to ensure that sampling effort is necessarily equal between Kelly's survey and ours. Consequently, the overall apparent balance between immigration and extinction in these analyses—i.e., the mean observed rates of immigration and extinction—are not necessarily representative of the true balance.

Results

Main model results

Sites that gained more neighborhood habitat had greater proportional species richness changes—i.e., richness changes were more positive or less negative (Fig. 3; $p<0.01$). A 1 ha increase in neighborhood habitat gain corresponds to an 0.8% increase in proportional species richness change. If our causal assumptions are valid (see Methods), then this value represents the causal effect of neighborhood habitat gains on species richness changes. This result comes from the model most favored by AICc, which used a 0.2 km neighborhood habitat radius. Our models built with other neighborhood habitat radii all yielded AICc values greater by 9 or more, indicating strong support for the 0.2 km radius.

In addition to the effect of neighborhood habitat changes on the index of species richness change, our regression analysis yielded some weak associations with other predictors. These parameters were not target causal estimands, so they do not necessarily have intuitive causal interpretations. Their 95% confidence intervals are shown in black in Fig. 3.

Alternate model results

When we refit our main model using a log-transformed version of the sampling effort ratio covariate, we found nearly identical results, which are given in Supplementary Table S3. As above, the model favored by AICc used a neighborhood radius of 0.2 km.

When we refit our main model using rarefied data with the effort ratio covariate omitted, we found qualitatively similar results with a weaker estimated effect size. A 1 ha increase in neighborhood habitat gain corresponds to a 0.3% increase in proportional species richness change ($p=0.08$). Full results are given in Supplementary Table S4. As above, the model favored by AICc used a neighborhood radius of 0.2 km.

When we modeled rarefied species richness as a time series, we again found that species richness increases with neighborhood habitat (Supplementary Table S5; $p<0.01$). A 1 ha difference in neighborhood habitat corresponds to an increase of 0.022 in species richness. AICc favored neighborhood radii of 0.1 and 0.2 km nearly equally. For consistency with the other three analyses, here we report results for the 0.2 km model. Results for the 0.1 km model are nearly identical and are given in Supplementary Table S6.

Supplementary Table S7 shows standardized estimates of the habitat gain effect for all four model structures across all seven neighborhood buffer radii.

Local extinction and immigration

When we rebuilt our statistical model with immigration rate or extinction rate as the response, we found a significant effect of neighborhood habitat gains on immigration rates (0.0025 increase in immigration rate per 1 ha; $p<0.01$) but not extinction rates. See Fig. 4. The estimated net “extinction” rate over the 41-year study interval was 0.52 species lost per species present at baseline. The estimated net immigration rate was 0.15 species gained per species present at baseline. These values are not estimates of the true extinction and immigration rates, as the data used for these analyses were rarefied using the site with the lowest ratio of 2011 versus 1970 sampling effort as a benchmark (see Methods). Thus, the absolute estimates of system-wide mean extinction and immigration rates are not biologically meaningful, and the extinction rate estimate in particular is almost certainly a large overestimate. Rather, the value in these analyses is their ability to highlight relative variation among sites in rate estimates.

Discussion

To our knowledge, we provide the first direct, longitudinal evidence for the Habitat Gain Hypothesis. In Banks Peninsula forest reserves, species richness changes between 1970 and 2011 increased with neighborhood habitat gains during the past century (Fig. 3). Over this 41-year study interval, relative changes in species richness are 0.8% greater with each 1 ha increase in neighborhood habitat gains. In our 26-reserve data set, the least and greatest neighborhood habitat changes differ by approximately 200 ha. This difference corresponds to a roughly 160% difference in proportional species richness changes. The models we used to estimate this effect control for potential confounding causal pathways, indicating that the association is causal, barring substantial uncontrolled confounding.

Our findings from Banks Peninsula are consistent with those of previous long-term studies that tracked habitat cover change and ecological community change. For example, a 15-year resurvey of dung beetle communities in the Amazon rainforest showed that differences in species composition decreased between forest fragments and intact forest sites as secondary forest regrew near fragments (Quintero & Roslin 2005). While these studies did not test the Habitat Gain Hypothesis directly, they—along with several other long-term studies and many space-for-time studies (Lindgren & Cousins 2017, Horváth et al. 2019, Brunet et al. 2021, Outhwaite et al. 2022)—suggest that increased neighborhood habitat amount could drive increased specialist species richness over time. Here we provide temporally explicit evidence. We also provide a new example of how understory plant species can become reestablished in newly restored forest patches over decadal scales (Stark et al. 2006), which has not always occurred in other systems (Holl & Crone 2004). Discrepancies between our study and others might owe to idiosyncratic variation in land use history.

The evidence reported here for the Habitat Gain Hypothesis can help inform management in fragmented landscapes. Global evidence suggests that biodiversity in habitat fragment reserves is susceptible to neighborhood habitat loss and degradation (Laurance et al. 2012, Horváth et al. 2019). Here we extend this finding to its inverse: appropriate neighborhood habitat restoration and regeneration can improve biodiversity outcomes in reserves.

It is not clear whether the positive effect of habitat gains on species richness is driven by immigration of new species or decreased extinction through rescue effects—i.e., immigration of conspecifics into pre-existing populations (Brown & Kodric-Brown 1977). Our data are not suitable for rigorous estimation of the true balance between extinction and immigration (see Methods), but our analyses suggest that immigration rates have responded more strongly to habitat gains than extinction rates (Fig. 4). This finding suggests that local habitat regeneration and restoration have helped species immigrate into Banks Peninsula reserves over recent decades. Some immigrants could be returning species that were previously extirpated. It is also possible that neighborhood habitat gains did provide rescue effects, thereby reducing extinction rates in reserves, but our analyses did not detect this effect. Future work could help refine these preliminary estimates of immigration and extinction rates and thereby clarify the demographic mechanisms driving biodiversity recovery.

Our results are also relevant to a longstanding debate regarding the effect of habitat fragmentation on biodiversity. Some authors contend that given a fixed amount of habitat, biodiversity will decline with the degree of fragmentation—i.e., the number of patches into which the habitat is divided, or a related metric (Haila 2002). Others contend that biodiversity is unaffected by fragmentation (Fahrig 2013) or sometimes positively affected (Riva & Fahrig 2023). On Banks Peninsula, most forest regeneration and restoration that occurred during our study interval has come in relatively small, disconnected patches (Fig. 1). Our results suggest that these patches have functioned as stepping stones for immigration of understory plants into mature forest reserves, thereby boosting reserve-scale species richness (although see below). It is beyond the scope of our study to address the fragmentation debate directly, but our results illustrate one way in which small, disjunct habitat patches can play a valuable role in conservation (Riva & Fahrig 2022).

We used multiple radii to define the habitat neighborhood, ranging from 100 m to 6 km, and a relatively short radius—200 m—was favored by AICc. This finding suggests that short-range dispersal is an important process driving seed input into reserves. Some species in our study system depend strongly on animal dispersal, and compared to other global bioregions, Aotearoa New Zealand has experienced especially severe declines in animal seed dispersers over the past millenium (Anderson et al. 2006, Kelly et al. 2010). The patterns we found may be indicative of substantial dispersal limitation in Banks Peninsula forest understory plants. It is also possible that the strong pattern we found using a small buffer radius reflects the influence of an unmeasured confounder. For example, if our measured covariates did not adequately capture some facet of spatial variation in conservation efforts, then this unmeasured confounder could have influenced both species richness in the reserve and forest cover adjacent to the reserve. Nonetheless, it is striking that neighborhood habitat gains are associated with estimated immigration rates but not extinction rates—consistent with a stepping stone model, as described above. Furthermore, although the 200 m buffer model was favored, we still found generally positive effects—albeit with greater uncertainty—using larger buffers like 6 km (Table S7). These findings suggest that propagule input from outside our focal reserves at least partially drives the observed changes in species richness.

It would also be valuable to explore the effects of habitat gains on species richness at the scale of the full Banks Peninsula landscape. Our results at the scale of single forest fragment reserves suggest that increasing habitat cover across the landscape could increase landscape-scale species richness. However, this prediction is a cross-scale extrapolation that must be tested at the appropriate scale (Riva & Fahrig 2023, Fletcher et al. 2023). Because our data are not suitable for estimating absolute changes in species richness, it is beyond the scope of this study to estimate richness changes at the scale of the full landscape—i.e., gamma diversity. Consequently, it would also be inappropriate to analyze changes in beta diversity, the ratio between gamma and alpha. Subsequent repeat survey work, following our new, repeatable survey protocol, could help fill this knowledge gap.

Habitat restoration efforts are expanding globally (Suding 2011, Brancalion et al. 2019), and to maximize the biodiversity benefits, it is necessary to understand how taxa respond to complex trajectories of habitat loss and gain. Here we provide new, temporally explicit evidence for a hypothesis that is often taken for granted: species richness in a habitat fragment can be increased by adding habitat to its local neighborhood. Much remains to be learned about biotic responses to dynamic habitat cover, such as the role of species functional and life history traits (Grass et al. 2018, Albaladejo-Robles et al. 2023), climate (Orrock et al. 2023), the magnitude of historical habitat loss (Gawecka & Bascompte 2021, 2023), patch shape and configuration (Tilman et al. 1997, Fahrig 2013, Huxel & Hastings 1999, Gawecka & Bascompte 2021, 2023), the duration of habitat loss and recovery phases, habitat quality (Tilman et al. 1997), and the suitability of the intervening habitat matrix (Resasco & Fletcher 2021, Leite et al. 2022). As our Banks Peninsula field study demonstrates, historical ecology methods can provide a temporally explicit empirical perspective that might not be attainable through other methods. With the UN Decade on Restoration underway, now is an opportune time to optimize the biodiversity benefits of habitat gains.

Data Availability Statement

All data and R scripts are available at https://zenodo.org/doi/10.5281/zenodo.11193308.

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Figures

Fig. 1

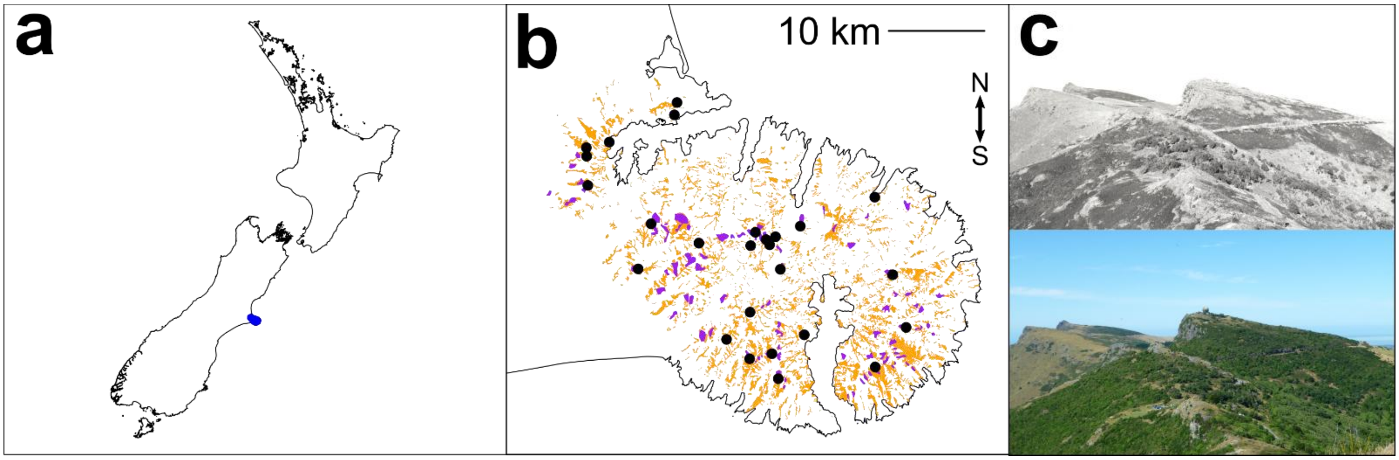

Fig. 1 Legend: Study region: Banks Peninsula-Te Pātaka o Rākaihautū, South Island, Aotearoa New Zealand. **a)** Mainland Aotearoa New Zealand with study region, Banks Peninsula, shown in blue. **b)** Purple polygons show 1920 forest cover, and orange polygons show forest regenerated between 1920 and 2012. Black points show study sites. **c)** An example of forest regeneration on Banks Peninsula shown by before and after photos of the landscape outside Kennedy's Bush Scenic Reserve. Upper photo (Geoff Kelly, used with permission) taken in 1970. Lower photo taken by the authors in 2011.

Fig. 2

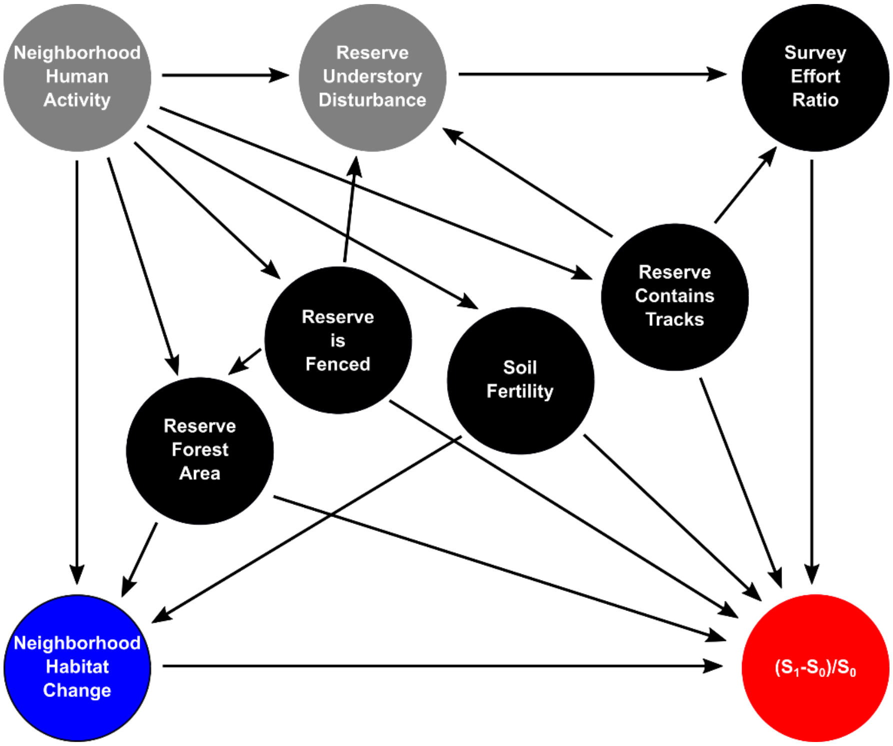

Fig. 2 Legend: Directed acyclic graph (DAG) used to select covariates for estimating the effect of neighborhood habitat area changes on index of species richness change. Covariates are selected to block “back door” confounding causal pathways that can create spurious associations in the data. The blue circle denotes our independent variable. The red circle denotes our dependent variable. Black circles denote other variables that were measured, and gray circles denote unmeasured variables. The index of species richness change is represented by $(S_1-S_0)/S_0$, where S denotes observed species richness, and the 0 or 1 subscript denotes the baseline or repeat survey. Neighborhood human activity is difficult to quantify but may affect ecological processes relevant to the study system. Reserve forest area is the area of forest in each reserve. Soil fertility describes soil conditions in each reserve based on field assessments. “Reserve is fenced” and “Reserve contains tracks” are binary variables. Reserve understory density could affect each surveyor’s ability to move through reserves and detect plant species. The ratio of survey effort between baseline and repeat census affects the apparent change in species richness, so when rarefaction is not used, it must be controlled for statistically. Alternative methods use rarefaction to remove this variable’s influence from the data before regression analysis.

Fig. 3

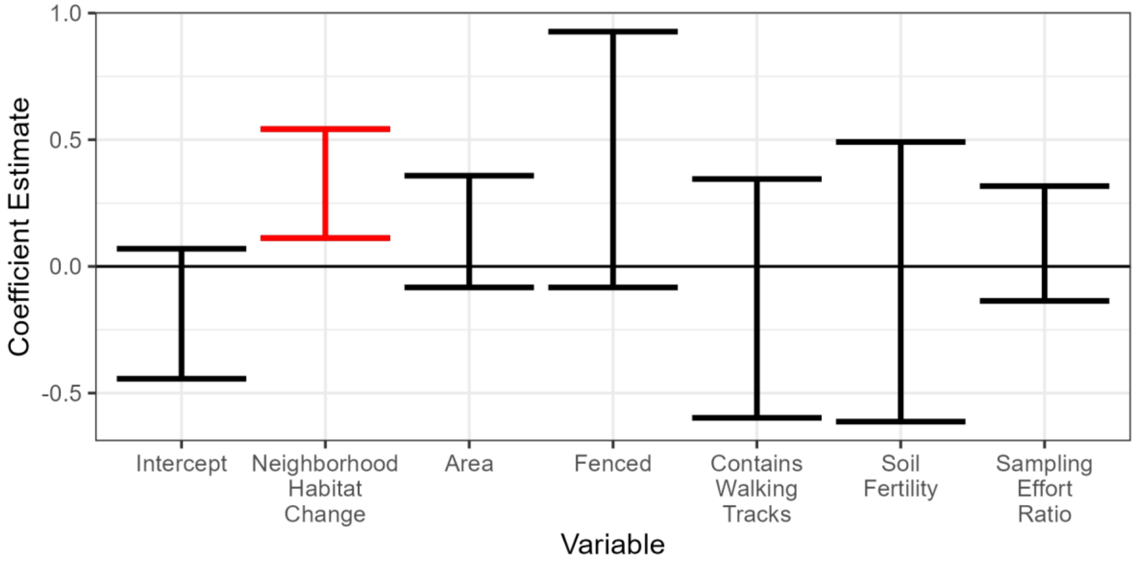

Fig. 3 Legend: 95% confidence intervals for coefficient estimates in regression models of understory plant species richness changes in Banks Peninsula forest reserves. Continuous predictors were centered and scaled (mean zero, SD 1), so coefficients reflect standardized effect sizes. The coefficient for neighborhood habitat area change (red), our target estimand, represents the causal effect on the index of species richness change. Other covariates were included as an adjustment set for the target estimand, so their coefficients do not necessarily represent causal effects.

Fig. 4

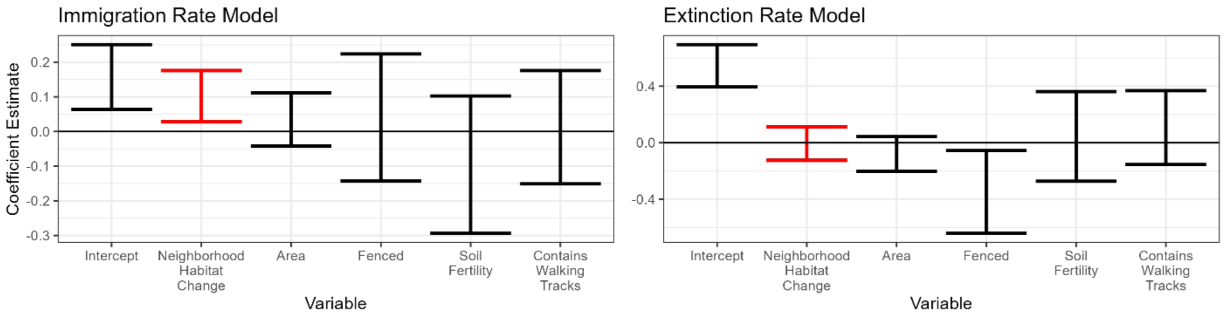

Fig. 4 Legend: 95% confidence intervals for coefficient estimates in regression models of immigration rates and extinction rates in Banks Peninsula forest reserves. Continuous predictors were centered and scaled (mean zero, SD 1), so coefficients reflect standardized effect sizes. The coefficient for neighborhood habitat area change (red), our target estimand, represents the causal effect on immigration or extinction rates. Other covariates were included as an adjustment set for the target estimand, so their coefficients do not necessarily represent causal effects.

Rosenblad & Sullivan (2025) Supplementary Information

Table S1: Banks Peninsula plant species in the data set with habitat use designations and references for habitat information.

Species	Forest specialist	Reference
Acaena anserinifolia	no	Wilson (2013)
Acaena caesiiglauca	no	Wilson (2013)
Acaena dumicola	no	Wilson (2013)
Aciphylla aurea	no	Wilson (2013)
Aciphylla subflabellata	no	Wilson (2013)
Alectryon excelsus	yes	Wilson (2013)
Anaphalioides bellidioides	no	Wilson (2013)
Anisotome aromatica	no	Wilson (2013)
Aristotelia fruticosa	no	Wilson (2013)
Aristotelia serrata	no	Wilson (2013)
Arthropodium candidum	no	Wilson (2013)
Asplenium appendiculatum	no	Wilson (2013)
Asplenium bulbiferum	no	Wilson (2013)
Asplenium flabellifolium	no	Wilson (2013)
Asplenium flaccidum	yes	Wilson (2013)
Asplenium hookerianum	no	Wilson (2013)
Asplenium lyallii	no	Wiser (2001)
Asplenium oblongifolium	no	Wilson (2013)
Asplenium richardii	no	Wilson (2013)
Astelia fragrans	no	Wilson (2013)
Australina pusilla	yes	Flora of NZ
Blechnum chambersii	no	Wilson (2013)
Blechnum colensoi	yes	Wilson (2013)
Blechnum discolor	yes	Wilson (2013)
Blechnum fluviatile	no	Wilson (2013)
Blechnum minus	no	Wilson (2013)
Blechnum novae-zelandiae	no	Chambers & Farrant (1998)
Blechnum penna-marina	no	Wilson (2013)
Blechnum procerum	no	Wilson (2013)
Blechnum vulcanicum	no	Wilson (2013)
Brachyglottis lagopus	no	Wilson (2013)
Brachyglottis sciadophila	yes	Wilson (2013)
Calystegia tuguriorum	no	Wilson (2013)
Cardamine debilis agg.	no	Flora of NZ
Carex breviculmis	no	Wilson (2013)

Carex forsteri	no	Wilson (2013)
Carex geminata	no	Wilson (2013)
Carex maorica	no	Flora of NZ
Carex secta	no	Wilson (2013)
Carex virgata	no	Wilson (2013)
Carex wakatipu	no	Flora of NZ
Carmichaelia australis	no	Wilson (2013)
Carpodetus serratus	yes	Wilson (2013)
Celmisia gracilenta	no	Wilson (2013)
Celmisia mackaui	no	Wilson (2013)
Cheilanthes sieberi	no	Wilson (2013)
Chionochloa conspicua	no	Wilson (2013)
Chionochloa rigida	no	Wilson (2013)
Clematis afoliata	no	Wilson (2013)
Clematis foetida	no	Wilson (2013)
Clematis paniculata	yes	Wilson (2013)
Colobanthus strictus	no	Wilson (2013)
Convolvulus waitaha	no	Wilson (2013)
Coprosma acerosa	no	Flora of NZ
Coprosma areolata	no	Wilson (2013)
Coprosma ciliata	no	Flora of NZ
Coprosma crassifolia	no	Wilson (2013)
Coprosma dumosa	no	Wilson (2013)
Coprosma linariifolia	no	Wilson (2013)
Coprosma lucida	no	Wilson (2013)
Coprosma propinqua	no	Wilson (2013)
Coprosma rhamnoides	no	Wilson (2013)
Coprosma rigida	no	Wilson (2013)
Coprosma robusta	no	Wilson (2013)
Coprosma rotundifolia	no	Wilson (2013)
Coprosma rubra	no	Wilson (2013)
Coprosma Tayloriae	no	Glenny & Cruickshank (2011)
Coprosma virescens	no	Wilson (2013)
Coprosma wallii	no	Flora of NZ
Coprosma x cunninghamii	no	Wilson (2013)
Cordyline australis	no	Wilson (2013)
Cordyline indivisa	yes	Wilson (2013)
Coriaria arborea	no	Wilson (2013)
Coriaria sarmentosa	no	Flora of NZ
Corokia cotoneaster	no	Wilson (2013)
Cortaderia richardii	no	Wilson (2013)
Corybas trilobus	no	Wilson (2013)
Crassula sieberiana	no	Wilson (2013)

Ctenopteris heterophylla	no	Wilson (2013)
Cyathea colensoi	no	Wilson (2013)
Cyathea dealbata	yes	Wilson (2013)
Cyathea smithii	yes	Wilson (2013)
Cyathodes juniperina	no	Wilson (2013)
Dacrycarpus dacrydioides	yes	Wilson (2013)
Dacrydium cupressinum	yes	Wilson (2013)
Deyeuxia avenoides	no	Flora of NZ
Dianella nigra	no	Wilson (2013)
Dichelachne crinita	no	Wilson (2013)
Dichondra repens	no	Flora of NZ
Dicksonia squarrosa	yes	Wilson (2013)
Discaria toumatou	no	Wilson (2013)
Dodonaea viscosa	no	Wilson (2013)
Dracophyllum acerosum	no	Wilson (2013)
Earina autumnalis	no	Wilson (2013)
Einadia allanii	no	Wilson (2013)
Elaeocarpus hookerianus	yes	Wilson (2013)
Elymus solandri	no	Wilson (2013)
Epilobium rotundifolium	no	Flora of NZ
Euchiton audax	no	Thorsen et al. (2011)
Festuca actae	no	Wilson (2013)
Festuca novae-zelandiae	no	Wilson (2013)
Fuchsia excorticata	no	Wilson (2013)
Fuchsia perscandens	no	Wilson (2013)
Galium propinquum	no	Wilson (2013)
Gaultheria antipoda	no	Wilson (2013)
Gaultheria depressa	no	Wilson (2013)
Gentianella grisebachii	no	Wilson (2013)
Geranium microphyllum	no	Wilson (2013)
Geranium sessiliflorum	no	Flora of NZ
Gingidia enysii	no	Wilson (2013)
Gingidia montana	no	Wilson (2013)
Gonocarpus incanus	no	Flora of NZ
Grammitis billardierei	no	Wilson (2013)
Grammitis poeppigiana	no	Wilson (2013)
Griselinia littoralis	no	Wilson (2013)
Gunnera monoica	no	Flora of NZ
Haloragis erecta	no	Wilson (2013)
Hebe salicifolia	no	Wilson (2013)
Hebe strictissima	no	Wilson (2013)
Hedycarya arborea	yes	Wilson (2013)
Helichrysum filicaule	no	Wilson (2013)

Helichrysum lanceolatum	no	Wilson (2013)
Heliohebe lavaudiana	no	Wilson (2013)
Hierochloe redolens	no	Wilson (2013)
Histiopteris incisa	no	Flora of NZ
Hoheria angustifolia	no	Wilson (2013)
Hydrocotyle elongata	no	Flora of NZ
Hydrocotyle heteromeria	no	Partridge (1989)
Hydrocotyle moschata	no	Flora of NZ
Hydrocotyle novae-zelandiae	no	Flora of NZ
Hymenophyllum atrovirens	yes	Flora of NZ
Hymenophyllum bivalve	yes	Wilson (2013)
Hymenophyllum demissum	yes	Wilson (2013)
Hymenophyllum dilatatum	yes	Wilson (2013)
Hymenophyllum flabellatum	yes	Flora of NZ
Hymenophyllum peltatum	yes	Flora of NZ
Hymenophyllum sanguinolentum	no	Wilson (2013)
Hymenophyllum villosum	no	Flora of NZ
Hypolepis ambigua	no	Brownsey & Chinnock (1984)
Hypolepis millefolium	no	Brownsey & Chinnock (1984)
Hypolepis rufobarbata	no	Brownsey & Chinnock (1984)
Ileostylus micranthus	no	Wilson (2013)
Isolepis habra	no	Wilson (2013)
Juncus edgariae	no	Wilson (2013)
Juncus planifolius	no	Flora of NZ
Kelleria dieffenbachii	no	Wilson (2013)
Korthalsella lindsayi	no	Wilson (2013)
Kunzea ericoides	no	Wilson (2013)
Lachnagrostis filiformis	no	Flora of NZ
Lachnagrostis pilosa	no	Wilson (2013)
Lagenifera pinnatifida	no	Wilson (2013)
Lagenifera pumila	no	Wilson (2013)
Lagenifera strangulata	yes	Wilson (2013)
Lastreopsis glabella	yes	Wilson (2013)
Lastreopsis velutina	yes	Wilson (2013)
Lemna minor	no	Wilson (2013)
Leptinella dioica	no	Wilson (2013)
Leptinella minor	no	Wilson (2013)
Leptinella squalida	no	Wilson (2013)
Leptolepia novae-zelandiae	yes	Wilson (2013)
Leptopteris hymenophylloides	yes	Wilson (2013)
Leptospermum scoparium	no	Flora of NZ
Leucopogon fraseri	no	Wilson (2013)
Libertia ixioides	no	Wilson (2013)

Libocedrus bidwillii	no	Wilson (2013)
Linum monogynum	no	Wilson (2013)
Lophomyrtus obcordata	no	Wilson (2013)
Luzula banksiana	no	Wilson (2013)
Luzula rufa	no	Wilson (2013)
Lycopodium australianum	no	Wilson (2013), Flora of NZ
Lycopodium fastigiatum	no	Wilson (2013)
Lycopodium scariosum	no	Flora of NZ
Lycopodium varium	no	Wilson (2013)
Lycopodium volubile	no	Flora of NZ
Macropiper excelsum	no	Wilson (2013)
Melicope simplex	no	Wilson (2013)
Melicytus alpinus	no	Wilson (2013)
Melicytus micranthus	yes	Flora of NZ
Melicytus ramiflorus	yes	Wilson (2013)
Mentha cunninghamii	no	Flora of NZ
Metrosideros diffusa	yes	Wilson (2013)
Microlaena avenacea	no	Wilson (2013)
Microsorum pustulatum	no	Wilson (2013)
Microtis unifolia	no	Wilson (2013)
Muehlenbeckia australis	no	Wilson (2013)
Muehlenbeckia complexa	no	Wilson (2013)
Myoporum laetum	no	Wilson (2013)
Myosotis "lytteltonensis"	no	Wilson (2013)
Myrsine australis	no	Wilson (2013)
Myrsine divaricata	no	Wilson (2013)
Neomyrtus pedunculata	no	Flora of NZ
Nertera depressa	no	Flora of NZ
Nothofagus fusca	yes	Wilson (2013)
Nothofagus solandri	yes	Wilson (2013)
Olearia avicenniifolia	no	Flora of NZ
Olearia ilicifolia	no	Wilson (2013)
Olearia nummulariifolia	no	Wilson (2013)
Olearia paniculata	no	Wilson (2013)
Ophioglossum coriaceum	no	Flora of NZ
Ourisia lactea	no	Wilson (2013)
Oxalis exilis	no	Wilson (2013)
Paesia scaberula	no	Flora of NZ
Parahebe lyallii	no	Wilson (2013)
Parsonsia capsularis	no	Flora of NZ
Parsonsia heterophylla	no	Wilson (2013)
Passiflora tetrandra	yes	Wilson (2013)
Pelargonium inodorum	no	Wilson (2013)

Pellaea rotundifolia	no	Wilson (2013)
Pennantia corymbosa	no	Wilson (2013)
Pentachondra pumila	no	Wilson (2013)
Phormium cookianum	no	Wilson (2013)
Pittosporum eugenioides	yes	Wilson (2013)
Pittosporum tenuifolium	no	Wilson (2013)
Plagianthus regius	no	Wilson (2013)
Plantago raoulii	no	Wilson (2013)
Pneumatopteris pennigera	yes	Wilson (2013)
Poa anceps	no	Wilson (2013)
Poa cita	no	Wilson (2013)
Poa colensoi	no	Wilson (2013)
Poa matthewsii	no	Wilson (2013)
Podocarpus hallii	no	Wilson (2013)
Podocarpus totara	no	Wilson (2013)
Polygonum salicifolium	no	Flora of NZ
Polystichum richardii	no	Wilson (2013)
Polystichum vestitum	no	Wilson (2013)
Pratia angulata	no	Flora of NZ
Prumnopitys ferruginea	yes	Wilson (2013)
Prumnopitys taxifolia	no	Wilson (2013)
Pseudognaphalium luteoalbum agg	no	Flora of NZ
Pseudopanax arboreus	no	Wilson (2013)
Pseudopanax colensoi	no	Wilson (2013)
Pseudopanax crassifolius	no	Wilson (2013)
Pseudowintera colorata	no	Wilson (2013)
Pteridium esculentum	no	Wilson (2013)
Pterostylis alobula	no	Flora of NZ
Pterostylis areolata	no	Wilson (2013)
Pterostylis banksii	yes	Flora of NZ
Pterostylis foliata	no	Flora of NZ
Pterostylis graminea	no	Wilson (2013)
Pterostylis tristis	no	Wilson (2013)
Pyrrosia eleagnifolia	no	Wilson (2013)
Ranunculus foliosus	no	Wilson (2013)
Ranunculus multiscapus	no	Wilson (2013)
Ranunculus reflexus	no	Wilson (2013)
Raoulia glabra	no	Wilson (2013)
Raoulia subsericea	no	Wilson (2013)
Raukaua anomalus	no	Wilson (2013)
Ripogonum scandens	yes	Wilson (2013)
Rubus cissoides	no	Wilson (2013)

Rubus schmidelioides	no	Wilson (2013)
Rubus squarrosus	no	Wilson (2013)
Rytidosperma clavatum	no	Wilson (2013)
Rytidosperma gracile	no	Flora of NZ
Rytidosperma setifolium	no	Flora of NZ
Rytidosperma unarede	no	Wilson (2013)
Scandia geniculata	no	Wilson (2013)
Schefflera digitata	yes	Wilson (2013)
Schizeilema trifoliolatum	no	Flora of NZ
Schoenus pauciflorus	no	Flora of NZ
Scleranthus biflorus	no	Wilson (2013)
Scleranthus uniflorus	no	Wilson (2013)
Senecio glaucophyllus	no	Wilson (2013)
Senecio glomeratus	no	Wilson (2013)
Senecio hispidulus	no	Flora of NZ
Senecio lautus	no	Flora of NZ
Senecio minimus	no	Wilson (2013)
Senecio wairauensis	no	Wilson (2013)
Solanum aviculare	no	Wilson (2013)
Solanum laciniatum	no	Wilson (2013)
Sophora microphylla	no	Wilson (2013)
Sophora prostrata	no	Wilson (2013)
Stellaria parviflora	no	Wilson (2013)
Streblus heterophyllus	yes	Wilson (2013)
Tetragonia tetragonioides	no	Flora of NZ
Tetragonia trigyna	no	Flora of NZ
Teucridium parvifolium	no	Wilson (2013)
Thelymitra longifolia	no	Wilson (2013)
Tmesipteris horomaka	yes	Perrie et al. (2010)
Tmesipteris tannensis	yes	Wilson (2013), Perrie et al. (2010)
Trichomanes venosum	yes	Wilson (2013)
Tupeia antarctica	no	Wilson (2013)
Uncinia affinis	yes	Flora of NZ
Uncinia banksii	no	Flora of NZ
Uncinia clavata	no	Flora of NZ
Uncinia ferruginea	uncertain	Wilson (2013), Flora of NZ
Uncinia leptostachya	no	Wilson (2013)
Uncinia rubra	no	Wilson (2013)
Uncinia scabra	no	Flora of NZ
Uncinia silvestris	yes	Flora of NZ
Uncinia uncinata	no	Wilson (2013)
Urtica ferox	no	Wilson (2013)
Urtica incisa	no	Wilson (2013)

Viola cunninghamii	no	Wilson (2013)
Viola filicaulis	no	Wilson (2013)
Vittadinia australis	no	Wilson (2013)
Wahlenbergia albomarginata	no	Wilson (2013)
Wahlenbergia gracilis	no	Wilson (2013)

Table S2: Correlation matrix of predictor variables used in regression models of species richness changes in Banks Peninsula reserves. NHC = neighborhood habitat area change (0.2 km radius). RHA = reserve forest area. RF (binary) = reserve is fenced. RCT (binary) = reserve contains walking tracks. SF = soil fertility. SCR = sampling effort ratio.

	NHC	**RFA**	**RF**	**RCT**	**SF**	**SER**
NHC		-0.06	0.17	-0.13	0.03	0.28
RFA	-0.06		-0.10	-0.14	-0.34	-0.29
RF	0.17	-0.10		0.10	0.01	0.00
RCT	-0.13	-0.14	0.10		0.31	0.25
SF	0.03	-0.34	0.01	0.31		0.02
SER	0.28	-0.29	0.00	0.25	0.02	

Table S3: Results from final model for OLS linear regression analysis of unrarefied data, using a log-transformed version of the Survey Effort Ratio covariate.

Parameter	**Estimate**	**Standard error**	**t**	**p**
Intercept	-0.19	0.11	-1.73	0.10
Neighborhood Habitat Change	0.30	0.10	3.05	0.01
Reserve Forest Area	0.17	0.10	1.82	0.08
Fence	0.46	0.23	2.01	0.06
Walking Tracks	-0.17	0.20	-0.85	0.40
Log(Survey Effort Ratio)	0.16	0.10	1.54	0.14

Table S4: Results from OLS linear regression analysis of rarefied data.

Parameter	**Estimate**	**Standard Error**	**t**	**p**
Intercept	-0.40	0.08	-5.06	0.00
Neighborhood Habitat Change	0.12	0.06	1.81	0.08
Reserve Forest Area	0.13	0.06	2.04	0.05
Fence	0.39	0.16	2.45	0.02

Walking Tracks	-0.14	0.14	-1.01	0.33

Table S5: Results for fixed effect parameters in generalized additive mixed model of rarefied data analyzed in the time series model structure. This model uses the 0.2 km neighborhood radius.

Parameter	Estimate	Standard Error	t	p
Intercept	6.38	0.38	16.68	0.00
Timepoint	-2.13	0.35	-6.08	0.00
Neighborhood Habitat Amount (0.2 km)	0.61	0.22	2.75	0.01
Reserve Forest Area	0.75	0.30	2.52	0.02
Fence	-1.10	0.68	-1.63	0.12
Walking Tracks	-0.46	0.58	-0.80	0.44
Neighborhood Habitat:Forest Area	0.08	0.24	0.35	0.73

Table S6: Results for fixed effect parameters in generalized additive mixed model of rarefied data analyzed in the time series model structure. This model uses the 0.1 km neighborhood radius.

Parameter	**Estimate**	**Standard Error**	**t**	**p**
Intercept	6.29	0.36	17.58	0.00
Timepoint	-1.94	0.35	-5.50	0.00
Neighborhood Habitat Amount (0.1 km)	0.56	0.20	2.74	0.01
Reserve Forest Area	0.78	0.27	2.84	0.01
Fence	-1.27	0.63	-2.03	0.06
Walking Tracks	-0.41	0.54	-0.75	0.46
Neighborhood Habitat:Forest Area	-0.25	0.31	-0.80	0.43

Table S7: Standardized estimates of the effect of neighborhood habitat gains from all models, using neighborhood buffer radii from 0.1 – 6 km. Model names denote the method used to control for sampling effort.

Model	**Buffer radius (km)**	**Estimate**	**Standard error**	**t**	**p**
Linear control	0.1	0.094	0.14	0.68	0.50
Linear control	0.2	0.33	0.10	3.2	0.0049
Linear control	0.5	-0.053	0.12	-0.42	0.68
Linear control	1	-0.045	0.12	-0.37	0.72
Linear control	2	0.12	0.13	0.93	0.37

Linear control	3	0.13	0.13	0.95	0.35
Linear control	6	0.14	0.16	0.88	0.39
Log control	0.1	0.066	0.13	0.51	0.61
Log control	0.2	0.30	0.10	3.0	0.0075
Log control	0.5	-0.036	0.12	-0.31	0.76
Log control	1	-0.019	0.11	-0.17	0.87
Log control	2	0.12	0.12	1.0	0.33
Log control	3	0.15	0.12	1.2	0.24
Log control	6	0.19	0.14	1.3	0.22
Rarefaction control	0.1	0.035	0.076	0.46	0.65
Rarefaction control	0.2	0.12	0.065	1.8	0.082
Rarefaction control	0.5	-0.062	0.070	-0.89	0.39
Rarefaction control	1	-0.052	0.070	-0.74	0.47
Rarefaction control	2	0.034	0.075	0.46	0.65
Rarefaction control	3	0.055	0.076	0.73	0.48
Rarefaction control	6	0.061	0.075	0.82	0.42
Rarefied time series	0.1	0.56	0.21	2.7	0.012
Rarefied time series	0.2	0.61	0.22	2.7	0.012
Rarefied time series	0.5	0.15	0.28	0.54	0.60
Rarefied time series	1	0.37	0.34	1.1	0.29
Rarefied time series	2	0.00	0.39	-0.01	0.99
Rarefied time series	3	-0.27	0.46	-0.59	0.56
Rarefied time series	6	-0.60	0.51	-1.2	0.25