

Research Article

Title: Neighbourhood forest regeneration promotes colonisation of remnant forests by native understorey plant species on Te Pātaka o Rākaihautū | Banks Peninsula

Keywords: habitat fragmentation, habitat loss, habitat restoration, habitat connectivity, habitat connectance, habitat amount, historical ecology, re-survey, forests

Authors: Kyle C. Rosenblad¹, Jon J. Sullivan²

Affiliations:

- 1- Department of Integrative Biology, University of California, Berkeley, USA
- 2- Department of Pest-Management and Conservation, AGLS, Lincoln University, Lincoln, New Zealand

Corresponding Author:

Kyle Rosenblad: kyle_rosenblad@berkeley.edu

Author Contributions

-Kyle Rosenblad: conceptualization, methodology, software, validation, formal analysis, investigation, data curation, writing – original draft, writing – review & editing, visualization, project administration, funding acquisition.

-Jon Sullivan: conceptualization, methodology, software, validation, investigation, resources, writing – review & editing, project administration, funding acquisition.

Funding: KCR's work was funded by a US Fulbright Fellowship and an NSF Graduate Research Fellowship.

Data and Code Availability: All data and code are available [here](#).

Ethics: This research did not involve animals.

Conflicts of Interest: None.

Abstract

Theory predicts that increasing habitat cover in the local landscape or “neighbourhood” of a habitat patch should increase colonisation rates over time. Although this prediction is widely invoked, empirical tests with longitudinal data are lacking. Here we tested this hypothesis using a 41-year repeat survey of 26 forest fragment reserves on Te Pātaka o Rākaihautū | Banks Peninsula, Aotearoa | New Zealand. Reserves with greater neighbourhood forest regeneration experienced greater native understorey plant species colonisation between 1970 and 2011. Evidence for positive effects on species richness was weak but directionally consistent. Overall, these findings provide rare longitudinal support for theoretical predictions linking neighbourhood habitat gains to community dynamics and highlight the conservation value of young secondary forest patches in fragmented landscapes.

Introduction

Habitat loss and fragmentation are driving losses of biodiversity worldwide (Haddad et al. 2015, Watson et al. 2018, Chase et al. 2020, Gonçalves-Souza et al. 2025). For many taxa, remaining habitat is confined to isolated patches in fragmented landscapes (Ewers et al. 2006, Prugh et al. 2008). In these landscapes, conservation outcomes might be improved by identifying and promoting ecological processes that positively influence the diversity of locally indigenous species persisting in remnant patches.

Most theories of habitat loss and fragmentation predict that patches with more habitat in their local landscapes or “neighbourhoods” will contain more habitat specialist species (MacArthur & Wilson 1963, Haila 2002, Fahrig 2013). Although these theories are typically applied to spatial comparisons among patches, they also imply a temporal prediction: increasing available habitat around an existing patch should positively influence colonisation rates and, ultimately, species richness within the patch over time (Tilman & Kareiva 1997, Farneda et al. 2015, García-Martínez et al. 2017, Newmark et al. 2023). Neighbourhood habitat gains might also reduce extinction rates via rescue effects—i.e., increased immigration of conspecifics (Brown & Kodric-Brown 1977). Longitudinal evidence for these predictions remains scarce. It is unclear to what extent, or how quickly, neighbourhood habitat restoration might reverse biodiversity declines owing to past habitat loss and fragmentation (Whytock et al. 2018).

The scarcity of longitudinal evidence on the effects of neighbourhood habitat regeneration owes partly to logistical difficulty. The proximal mechanisms of species richness change—colonisation and extinction—may occur slowly relative to the duration of typical field studies (Tilman & Kareiva 1997, Magurran et al. 2010, Watts et al. 2020). Thus, detecting community responses to habitat regeneration often requires data on both community composition and habitat cover spanning decades or more. Historical ecology approaches, which integrate legacy surveys with historical landscape reconstructions, may provide a way to assemble such data when conventional methods are not feasible (Vellend et al. 2013).

Te Pātaka o Rākaihautū | Banks Peninsula provides a rare opportunity to assess the influence of neighbourhood habitat regeneration on species turnover in remnant habitat patches over time (Fig. 1). Following human arrival, forest cover declined sharply until approximately 1920, followed by widespread secondary forest regeneration (Ogilvie 2007, Wilson 2009, Wilson 2013). Many of the oldest and largest remnant forest patches are now protected as Scenic Reserves or covenants. The indigenous flora of each Scenic Reserve was surveyed in 1970 (Kelly 1972), establishing a valuable baseline for assessing how long-term changes in native forest plant diversity have responded to local landscape changes.

Here, we tested the hypothesis that neighbourhood forest regeneration promotes increased colonisation, decreased extinction, and increased species richness of native understorey plant species in remnant forest patches. To test this hypothesis, we combined repeat botanical surveys from 26 Scenic Reserves on Te Pātaka o Rākaihautū with reconstructions of historical forest cover to quantify long-term changes in plant communities and neighbourhood habitat availability.

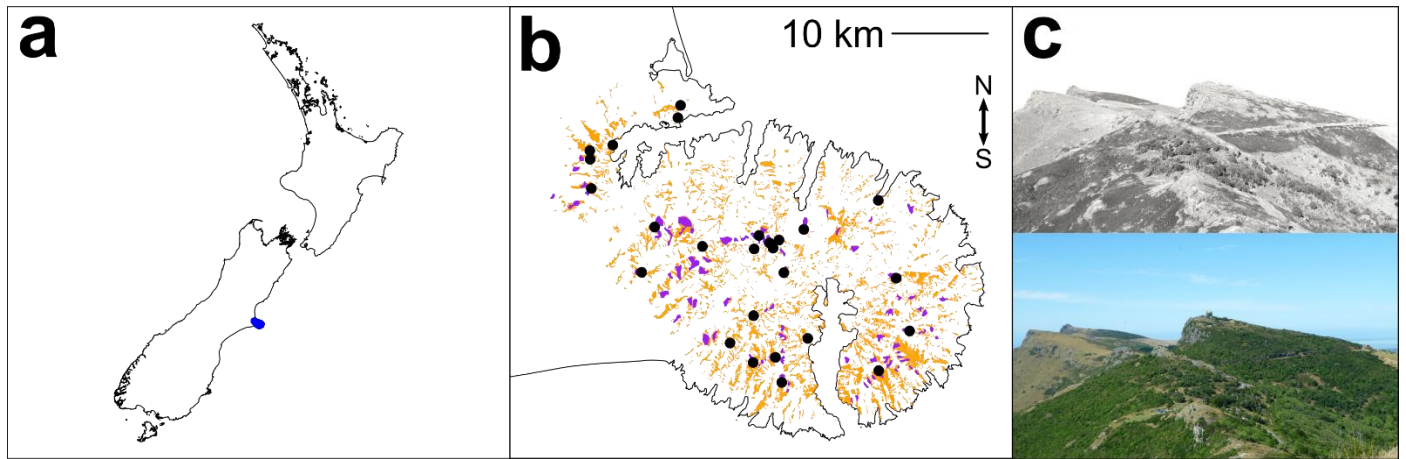


Fig. 1: Study region: Te Pātaka o Rākaihautū | Banks Peninsula. **a)** Mainland Aotearoa with study region shown in blue. **b)** Purple polygons show 1920 forest cover, and orange polygons show forest regenerated between 1920 and 2012 (Wilson 2013, LCDB v5.0 2018). Black points show study sites. **c)** Example of forest regeneration between 1970 (Geoff Kelly, used with permission) and 2011 (the authors).

Methods

Study area

Before anthropogenic deforestation began on Te Pātaka o Rākaihautū several centuries ago, this roughly 1,300 km² landscape was covered by nearly continuous evergreen forest (Wilson 2009, Wilson 2013). Following Māori arrival, portions of this forest were burned, and subsequent European settlement resulted in extensive additional clearing (Ogilvie 2007, Wilson 2009, Wilson 2013). By approximately 1920, only a small minority 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 (Ogilvie 2007, Wilson 2009, Wilson 2013, Fig. 1). Since then, a

combination of passive and active forest restoration has increased indigenous forest cover across the landscape (Wilson 2013).

Baseline survey

Focusing on native obligate forest-dwelling understorey plants, we used data from Kelly (1972) to characterise species occurrence in 1970 for 26 forest fragment reserves across Te Pātaka o Rākaihautū (including the Port Hills). Kelly (1972) surveyed each reserve using transect routes of varying lengths, which covered each habitat type 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. The exact routes (not documented) were designed haphazardly or pseudo-randomly, but independently of ease of access (G. Kelly pers. comm.). All native species observed were recorded. Survey effort was quantified by the total number of hours spent surveying each reserve.

Repeat survey

To characterise native understorey plant species occurrence 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.) We recorded all 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. See Appendix 1 for further detail regarding measures taken to promote comparability between the 1970 and 2011 datasets. Table S1 lists all species recorded in 1970 and/or 2011.

Quantifying neighbourhood habitat change

To account for potential lagged responses of native understorey plant communities to habitat change, we quantified neighbourhood change in forest cover relative to 1920, as shown in a historical map (Wilson 2013). We compared this to 2012 data from the New Zealand Landcover Database version 5.0 (LCDB v5.0 2018). We assume that the one-year gap between our 2011 survey and the 2012 habitat data had negligible influence on our analysis. See Appendix 1 for further details.

We used a buffer metric of neighbourhood forest cover (Prugh 2009, Watling et al. 2020), in which total forest area is summed within a given radius from the focal site. Following Watling et al. (2020), we computed six versions of this variable using buffer radii of 200 m, 500 m, 1 km, 2 km, 3 km, and 6 km. We compared the performance of these six buffer radii in our main analysis (see below) via AICc.

Statistical analyses

We used generalised additive models (GAMs) to analyse three response variables: colonisation, extinction, and change in species richness. In all models, we used a two-

dimensional smoothing spline over sites' spatial coordinates to account for spatial autocorrelation. Colonisation was quantified as the number of species present in 2011 and absent in 1970. We modeled colonisation using a restricted maximum likelihood GAM with a Tweedie error distribution. Extinction was quantified as the proportion of species present in 1970 that were absent in 2011. We modeled extinction using a Bayesian ordered beta GAM, which accommodates proportions including exact 0 and 1 values (Kubinec 2023). Species richness change was quantified proportionally—i.e., 2011 richness divided by 1970 richness—and modeled with a restricted maximum likelihood Tweedie GAM. (Continuous response distributions were used because our approach to summarising uncertainty in species identification yielded non-integer values for colonisation, extinction, and richness change. See Appendix 1.)

Each model included neighbourhood forest cover change and three additional covariates that could influence understorey plant community dynamics. These included reserve forest area (Kelly 1972), presence or absence of fencing, and presence or absence of walking tracks.

For each response variable, we fit two versions of the model. In one version, we controlled for temporal variation in sampling effort by including an additional covariate. This covariate was the ratio of total transect length surveyed in 2011 to adjusted survey effort in 1970. To estimate forest-specific sampling effort, survey effort in 1970 was multiplied by the proportion of each reserve classified as forest, as some reserves contain non-forest habitats that were included in Kelly's (1972) surveys. In the second

model version, sampling effort was standardised prior to analysis via rarefaction (see Appendix 1).

For each of the six basic models described above—comprising three response variables and two methods to account for sampling effort—we fit separate versions with each of the six neighbourhood buffer radii discussed above, which were compared via AICc. This approach yielded a total of 36 regression models (12 for each response variable).

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

Software

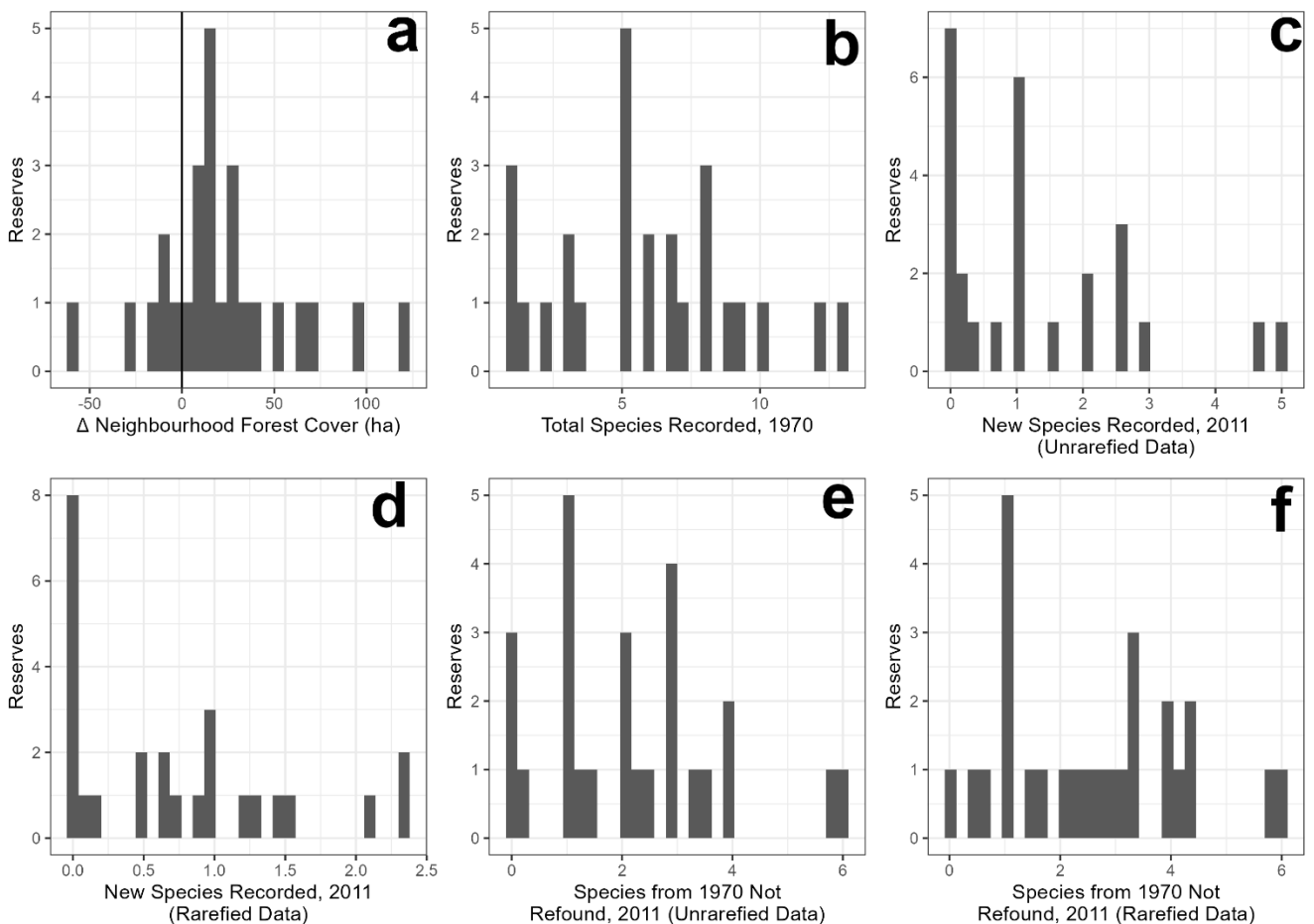
All analyses were done in R version 4.5.3 (R Core Team 2026). Restricted maximum likelihood GAMs were fit with mgcv (Wood 2011), and Bayesian GAMs were fit with brms (Bürkner 2017).

Results

Neighbourhood buffer radii

In the colonisation models (details below), radii of 200 m and 500 m were most favored by AICc (Table S3). For the non-rarefied data, AICc favored the 500 m buffer over the 200 m buffer by 1.3, whereas for the rarefied data, the 200m buffer was favored by only 0.1. Richness models showed little differentiation of AICc values across buffer radii (see Table S4), but 500 m again performed well. (Extinction showed little signal of

neighbourhood habitat effects; see below.) Thus for consistency, all main results reported here use the 500 m buffer. Alternative results using the 200 m buffer are reported in Tables S5-S10.



226

Fig. 2: Summaries of variables characterising neighborhood forest cover change and native forest understorey plant species turnover across 26 Banks Peninsula Scenic Reserves between 1970 and 2011. Temporal variation in sampling effort was controlled in two ways: one using rarefaction-based methods and one using regression-based methods. Both rarefied and unrarefied versions of the data are shown. (Non-integer

species count estimates.) **b-f)** *Non-integer values result from summarising uncertainty in field specimen identification (see Appendix 1).*

Changes in neighbourhood forest cover

For the 500 m buffer radius, the mean change in forest cover was a 22 ha increase, with values ranging from a 59 ha decrease to a 120 ha increase (Fig. 2a). 20 sites showed increases, while 6 showed decreases.

Colonisation

The mean number of new species encountered in 2011 for the unrarefied dataset was 1.3 (SD 1.4). The mean for the rarefied dataset was 0.7 (SD 0.7). (See Fig. 2c-d.) The number of new species encountered was positively associated with changes in neighbourhood forest cover for both the unrarefied data (Fig. 3, $p=0.007$) and the rarefied data (Fig. 3, $p=0.03$). Compared to zero neighbourhood regeneration, predicted colonisation for a reserve with 100 ha of regeneration was greater by 3.9 species. Tables S5-6 show coefficient estimates for other predictor variables in the colonisation models.

Extinction

The mean number of species from the 1970 survey not refound in the 2011 survey—“extinct species” for brevity—was 2.2 for the unrarefied dataset (SD 1.6). The mean for the rarefied dataset was 2.6 (SD 1.6). (See Fig. 2e-f.) Extinct species showed no clear

relationship with changes in neighbourhood forest cover for either the rarefied or
unrarefied data (Tables S7-8).

Richness

The mean number of species recorded in 1970 was 5.9 (SD 3.3). The mean in 2011
was 4.9 for the unrarefied data (SD 3.0) and 4.0 for the rarefied data (SD 2.6). Richness
change over time showed a weak positive association with changes in neighbourhood
forest cover for the unrarefied data (Table S9, $p=0.24$), and little clear signal for the
rarefied data. Tables S9-10 show coefficient estimates for other predictor variables.

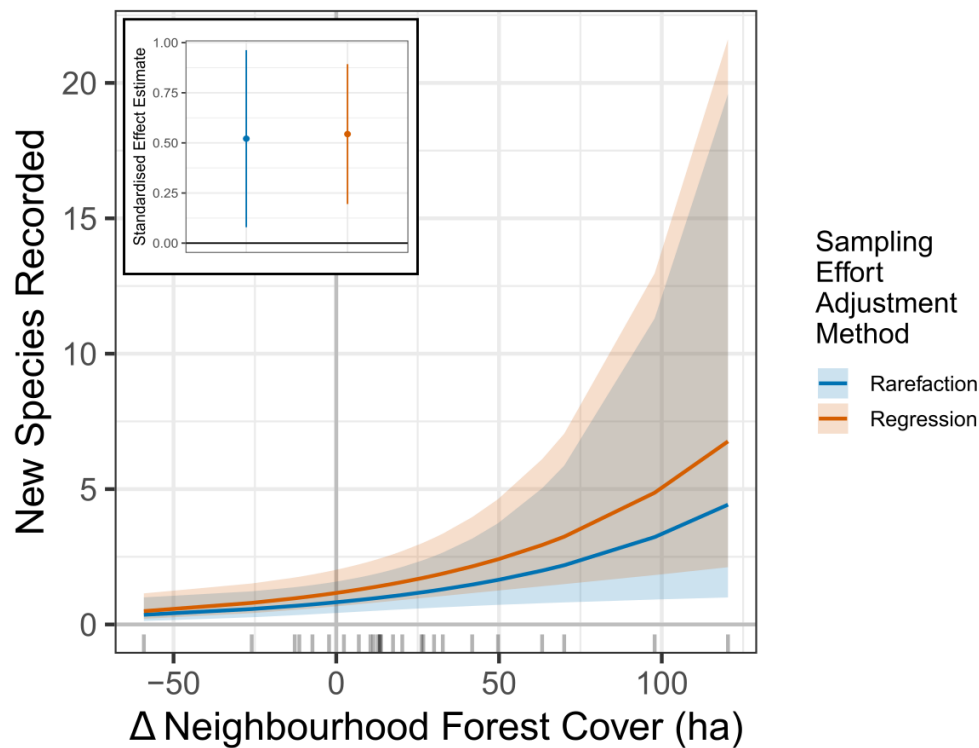


Fig. 3: Association between change in neighbourhood forest cover and number of new species recorded between 1970 and 2011. Conditional mean curves and 95% confidence bands were generated by Tweedie GAMs with a log link function. Inset shows point estimates and 95% confidence intervals for standardised effect sizes—the effect of a one-standard deviation (37 ha) increase in neighborhood habitat change. X-axis rug marks show the distribution of the data.

Discussion

Here we show, across 26 forest reserves on Te Pātaka o Rākaihautū, that native understorey plant species colonisation over 41 years increased with the degree of neighbourhood forest regeneration (Fig. 3). Compared to a reserve with no

278 neighbourhood regeneration, a reserve with 100 ha of neighbourhood regeneration was
279 expected to have 3.9 more new species recorded in 2011. These results suggest that
280 neighbourhood forest regeneration promoted colonisation of remnant patches over time.
281 Neighbourhood forest regeneration had no clear relationship with extinction (Tables S7-
282 8), whereas temporal changes in species richness were also positively associated with
283 neighbourhood habitat gains, although the signal was weaker (Tables S9-10). Overall,
284 these findings suggest that neighbourhood forest gains are increasing colonisation rates
285 of native understorey plant species in remnant forest fragments over time, which may
286 eventually lead to clearer patterns of increase in species richness.

287

288 More broadly, these findings help fill an important conceptual gap regarding the effects
289 of neighbourhood habitat gains on species turnover in remnant patches. Although
290 fragmentation theory predicts that increasing neighbourhood habitat should increase
291 colonisation and species richness through time (MacArthur & Wilson 1963, Haila 2002,
292 Fahrig 2013), most empirical support derives from spatial comparisons among patches
293 rather than temporal responses to habitat gains (García-Martínez et al. 2017, Lindgren
294 & Cousins 2017, Torrenta & Villard 2017, Watling et al. 2020). Longitudinal studies of
295 habitat loss have documented ensuing extinctions and richness declines (Ferraz et al.
296 2007, Horváth et al. 2019), but direct observations of the effects of neighbourhood
297 habitat gains remain scarce. Our results provide rare longitudinal evidence that
298 neighbourhood habitat gains can promote increased colonisation in remnant patches.

299

300 From a management perspective, these results suggest that forest regeneration near
301 remnant patches can contribute to biodiversity recovery by increasing colonisation of
302 native understorey plant species. Since peak deforestation in approximately 1920, most
303 forest regeneration on Te Pātaka o Rākaihautū has been passive, producing the small,
304 young secondary forest patches that now surround many older remnants (Wilson 2013,
305 Fig. 1). Our findings underscore that these secondary patches have conservation value
306 (Norton et al. 2018, Riva & Fahrig 2022). Even where regenerated forests are small or
307 relatively young, these patches may increase landscape connectivity and promote
308 colonisation of nearby reserves (Metzger et al. 2009, Fahrig 2020). This finding does
309 not diminish the importance of protecting large, old forest remnants (Norton & Miller
310 2000, Watson et al. 2018), but affirms that remnant protection can be complemented by
311 allowing, protecting, and (where appropriate) actively restoring secondary forest in the
312 surrounding landscape (Forbes et al. 2023). In addition to neighbourhood forest
313 regeneration, our results also provide longitudinal evidence for livestock exclusion
314 fencing as a tool to promote increased colonisation (Tables S5-6), decreased extinction
315 (Tables S7-8), and more positive species richness trends (Tables S9-10) in native
316 understorey plant communities, consistent with prior research (Burns et al. 2011).

317

318 A primary limitation of this study is that the 1970 and 2011 surveys differed in sampling
319 methods, necessitating retrospective harmonisation of the datasets. We approached
320 this task in two ways, including both rarefaction-based and regression-based controls
321 for survey effort. Our primary conclusion—that neighbourhood habitat gains promote
322 colonisation in remnant fragments—was robust to alternative assumptions regarding the

323 role of survey effort. Strength of support for our secondary hypothesis—that
324 neighbourhood habitat gains positively influence species richness over time—is weaker
325 and depends on the analytical method used to account for differences in survey effort.
326 Another important caveat is that the goal of harmonisation is simply to standardise the
327 degree of over-sampling or under-sampling relative to the 1970 baseline, such that fair
328 comparisons can be made across reserves regarding temporal change in species
329 assemblages. It is not possible to achieve equal absolute levels of sample
330 completeness between time points within each reserve. Thus our results can only
331 inform questions regarding relative comparisons across reserves—not absolute trends
332 in colonisation or richness over time.

333

334 Overall, our results indicate that colonisation of native understorey plant species into
335 remnant forest patches on Te Pātaka o Rākaihautū increased with neighbourhood
336 forest regeneration. Increased colonisation may have also promoted more favorable
337 trends in overall species richness. Our findings suggest an equivalent national-scale
338 analysis using National Vegetation Survey plot data could be informative. Together,
339 these findings highlight the conservation value of forest regeneration in fragmented
340 landscapes, including small and young secondary forest patches.

341

342 **Acknowledgements**

343 Geoff Kelly, Hugh Wilson, and David Glenny provided advice on field study design and
344 botanical specimen identification.

345

References

- Allan, HH 1961. Flora of New Zealand. Volume I. R. E. Owen, Government Printer, Wellington, New Zealand.
- Brown, JH & Kodric-Brown, A 1977. Turnover rates in insular biogeography: effect of immigration on extinction. *Ecology* 58: 445–449.
- Brownsey, PJ & Chinnock, RJ 1984. A taxonomic revision of the New Zealand species of *Hypolepis*. *New Zealand Journal of Botany* 22 (1): 43-80
- Bürkner, PC 2017. brms: An R Package for Bayesian Multilevel Models Using Stan. *Journal of Statistical Software* 80(1): 1-28. doi:10.18637/jss.v080.i01
- Burns BR, Floyd CG, Smale MC, Arnold GC 2011. Effects of forest fragment management on vegetation condition and maintenance of canopy composition in a New Zealand pastoral landscape. *Austral Ecology* 36: 153–166
- Chambers, TC & Farrant, PA 1998. The *Blechnum procerum* (“capense”) (Blechnaceae) complex in New Zealand. *New Zealand Journal of Botany* 36:1-19.
<http://dx.doi.org/10.1080/0028825X.1998.9512544>
- Chase, JM, Blowes, SA, Knight, TM, Gerstner, K, & May, F 2020. Ecosystem decay exacerbates biodiversity loss with habitat loss. *Nature* 584: 238-243.

369

370 Edgar, E & Connor, H 2000. Flora of New Zealand Volume V: Gramineae. Manaaki
371 Whenua Press, Lincoln, New Zealand.

372

373 Ewers, R M, Kliskey, AD, Walker, S, Rutledge, D, Harding, JS & Didham,
374 RK 2006. Past and future trajectories of forest loss in New Zealand. Biological
375 Conservation 133: 312-325.

376

377 Fahrig, L 2013. Rethinking patch size and isolation effects: the habitat amount
378 hypothesis. Journal of Biogeography 40: 1649-1663. <https://doi.org/10.1111/jbi.12130>

379

380 Farneda, FZ, et al. 2015. Trait-related responses to habitat fragmentation in Amazonian
381 bats. Journal of Applied Ecology 52: 1381-1391. [https://doi.org/10.1111/1365-](https://doi.org/10.1111/1365-2664.12490)
382 2664.12490

383

384 Ferraz, G, Nichols, JD, Hines, JE, Stouffer, PC, Bierregaard, RO & Lovejoy, TE 2007. A
385 large-scale deforestation experiment: effects of patch area and isolation on Amazon
386 birds. Science 315: 238-241.

387

388 Forbes AS, Richardson SJ, Carswell FE, Mason NWH, Burrows LE 2023. Knowing
389 when native regeneration is for you, and what you should do about it. The Aotearoa
390 New Zealand context. New Zealand Journal of Ecology 47: 3524.

391

392 García-Martínez, M, Valenzuela-González, JE, Escobar-Sarria, F, López-Barrera, F, &
 393 Castaño-Meneses, G 2017. The surrounding landscape influences the diversity of leaf-
 394 litter ants in riparian cloud forest remnants. PLoS One 12: Article e0172464,
 395 10.1371/journal.pone.0172464
 396
 397 Glenny D, & Cruickshank J 2011. Taxonomic notes on the New Zealand
 398 flora: *Coprosma dumosa* and *C. tayloriae*, are there two species? New Zealand Journal
 399 of Botany 49:481-488. doi: 10.1080/0028825X.2011.607832
 400
 401 Gonçalves-Souza, T et al. 2025. Species Turnover Does Not Rescue Biodiversity in
 402 Fragmented Landscapes. Nature 640: 702-706. [https://doi.org/10.1038/s41586-025-](https://doi.org/10.1038/s41586-025-08688-7)
 403 08688-7
 404
 405 Haddad, NM et al. 2015. Habitat fragmentation and its lasting impact on Earth's
 406 ecosystems. Science Advances 1: e1500052. doi: 10.1126/sciadv.1500052
 407
 408 Haila, Y 2002. A conceptual genealogy of fragmentation research: from island
 409 biogeography to landscape ecology. Ecological Applications 12: 321-334.
 410
 411 Horváth, Z, Ptacnik, R, Vad, CF & Chase, JM 2019. Habitat loss over six decades
 412 accelerates regional and local biodiversity loss via changing landscape connectance.
 413 Ecology Letters 22: 1019-1027. <https://doi.org/10.1111/ele.13260>
 414

415 Kelly, GC 1972. Scenic reserves of Canterbury. Botany Division, Department of
 416 Scientific and Industrial Research, New Zealand. 389 pp.
 417
 418 Kubinec, R 2023. Ordered Beta Regression: A Parsimonious, Well-Fitting Model for
 419 Continuous Data With Lower and Upper Bounds. *Political Analysis* 31: 519–536.
 420
 421 LCDB v5.0 (2018) [https://iris.scinfo.org.nz/layer/104400-lcdb-v50-land-cover-database-](https://iris.scinfo.org.nz/layer/104400-lcdb-v50-land-cover-database-version-50-mainland-new-zealand/)
 422 [version-50-mainland-new-zealand/](https://iris.scinfo.org.nz/layer/104400-lcdb-v50-land-cover-database-version-50-mainland-new-zealand/)
 423
 424 Lindgren, JP & Cousins, SA 2017. Island biogeography theory outweighs habitat
 425 amount hypothesis in predicting plant species richness in small grassland remnants.
 426 *Landscape Ecology* 32: 1895-1906. <https://doi.org/10.1007/s10980-017-0544-5>
 427
 428 MacArthur, RH & Wilson, EO 1963. An equilibrium theory of insular
 429 biogeography. *Evolution*, 17: 373-387.
 430
 431 Magurran, AE, Baillie, SR, Buckland, ST, Dick, JM, Elston, DA, Scott, EM, Smith,
 432 RI, Somerfield, PJ, & Watt, AD 2010. Long-term datasets in biodiversity research and
 433 monitoring: Assessing change in ecological communities through time. *Trends in Ecol-*
 434 *ogy & Evolution* 25: 574-582. <https://doi.org/10.1016/j.tree.2010.06.016>
 435

436 Newmark, WD, et al. 2023. Enhanced regional connectivity between western North
 437 American national parks will increase persistence of mammal species
 438 diversity. *Scientific Reports* 13: 474. <https://doi.org/10.1038/s41598-022-26428-z>
 439
 440 Norton, BDA & Miller, CJ 2000. Some issues and options for the conservation of native
 441 biodiversity in rural New Zealand. *Ecological Management & Restoration* 1: 26-
 442 34. <https://doi.org/10.1046/j.1442-8903.2000.00005.x>
 443
 444 Norton, DA, Butt, J & Bergin, DO 2018. Upscaling restoration of native biodiversity: A
 445 New Zealand perspective. *Ecological Management & Restoration* 19: 26-
 446 35. <https://doi.org/10.1111/emr.12316>
 447
 448 Ogilvie, G 2007. *Banks Peninsula, Cradle of Canterbury* (3rd edition). Phillips & King
 449 Publishers, Christchurch, NZ (284 pp.)
 450
 451 Partridge, TR 1989. Soil seed banks of secondary vegetation on the Port Hills and
 452 Banks Peninsula, Canterbury, New Zealand, and their role in succession. *New Zealand*
 453 *Journal of Botany* 27: 421-436.
 454
 455 Perrie, LR, Brownsey, PJ, & Lovis, JD 2010. *Tmesipteris horomaka*, a new octoploid
 456 species from Banks Peninsula. *New Zealand Journal of Botany* 48: 15-29.
 457

458 Prugh, LR, Hodges, KE, Sinclaer, ARE & Brashares, JS 2008. Effect of habitat area and
 459 isolation on fragmented animal populations. Proceedings of the National Academy of
 460 Science of the United States of America 105: 20770–20775.

461

462 Prugh, LR 2009. An evaluation of patch connectivity measures. Ecological Applications
 463 19: 1300-1310.

464

465 QGIS.org (2022). QGIS Geographic Information System. QGIS
 466 Association. <http://www.qgis.org>

467

468 R Core Team (2026). R: A Language and Environment for Statistical Computing. R
 469 Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>.

470

471 Riva, F & Fahrig, L 2022. The disproportionately high value of small patches for
 472 biodiversity conservation. Conservation Letters 15(3): e12881.

473

474 Thorsen, MJ, Seddon, PJ & Dickinson, KJM 2011. Faunal influences on New Zealand
 475 seed dispersal characteristics. Evolutionary Ecology 25: 1397-1426.

476

477 Tilman, D, Lehman, CL & Kareiva, P 1997. Population dynamics in spatial
 478 habitats. Pages 3 20 in D. Tilman P. Kareiva, editors. Spatial ecology. Princeton
 479 University Press, Princeton, New Jersey.

480

481 Torrenta, R & Villard, MA 2017. A test of the habitat amount hypothesis as an
 482 explanation for the species richness of forest bird assemblages. *Journal of*
 483 *Biogeography* 44: 1791-1801. <https://doi.org/10.1111/jbi.13022>
 484
 485 Vellend, M, Brown, CD, Kharouba, HM, McCune, JL & Myers-Smith, IH 2013. Historical
 486 ecology: Using unconventional data sources to test for effects of global environmental
 487 change. *American Journal of Botany* 100: 1294-
 488 1305. <https://doi.org/10.3732/ajb.1200503>
 489
 490 Watling, JI, et al. 2020. Support for the habitat amount hypothesis from a global
 491 synthesis of species density studies. *Ecology Letters* 23: 674-
 492 681. <https://doi.org/10.1111/ele.13471>
 493
 494 Watson, JEM et al. 2018. The exceptional value of intact forest ecosystems. *Nature*
 495 *Ecology & Evolution* 2: 599-610. <https://doi.org/10.1038/s41559-018-0490-x>
 496
 497 Watts, K et al. 2020. Ecological time lags and the journey towards conservation
 498 success. *Nature Ecology & Evolution* 4: 304-311. <https://doi.org/10.1038/s41559-019->
 499 1087-8
 500
 501 Whytock, RC et al. 2018. Bird-community responses to habitat creation in a long-term,
 502 large-scale natural experiment. *Conservation Biology* 32: 345-
 503 354. <https://doi.org/10.1111/cobi.12983>

504

505 Wilson, HD 2009. Natural history of Banks Peninsula. Canterbury University Press, New
506 Zealand.

507

508 Wilson HD 2013. Plant Life on Banks Peninsula. Cromwell, New Zealand: Manuka
509 Press.

510

511 Wiser, SK 2001. Montane rock outcrops: islands of biodiversity on Banks
512 Peninsula. Canterbury Botanical Society Journal 35: 32-36.

513

514 Wood, SN 2011. Fast stable restricted maximum likelihood and marginal likelihood
515 estimation of semiparametric generalized linear models. Journal of the Royal Statistical
516 Society (B) 73(1): 3-36