RestoratiON: a tool to identify priority restoration sites in Ontario

What does the tool do?

The RestoratiON tool allows a user to select a target landscape within Ontario, and for that area of interest, identify candidate areas for restoration that are currently considered degraded in some way. For each candidate area, the tool measures the potential benefit of restoration based on several metrics, including patch size, connectivity and environmental heterogeneity. Candidate areas within the target landscape are ranked in terms of their restoration benefit and are provided to the user to further assess their suitability for restoration activities.

What is degraded land?

The RestoratiON tool builds off previous efforts defining restorable areas (Currie et al. 2023) by referring to the human footprint as a multi-faceted expression of anthropogenic influence on an area (Hirsh-Pearson et al. 2022). The variables that contribute to the footprint are active mines, abandoned mines, night light pollution, oil and gas extraction, aggregate extraction, topsoil extraction, and marginal farmland. Given uncertainty in the magnitude of impact that would render an area degraded, the user can define thresholds that separate degraded from undegraded areas. For example, the user can choose the intensity of mining activity, intensity of night light pollution, and intensity of oil and gas extraction that would render an area degraded. An area is classified as degraded if any one variable meets its threshold.

What is restoration?

Restoration is the act of turning a degraded area into habitat. The tool prioritizes restorable sites across Ontario based on the benefit to biodiversity that would be realized after restoration occurs in a particular area. However, comparing candidate restoration areas across a region as large as Ontario is computationally unfeasible. Hence, restoration and its benefit must be calculated for smaller landscapes and then the benefit can be compared among landscapes.

How are candidate restoration areas defined?

To determine land cover classes across the province, Ontario is divided into 15 m x 15 m pixels; each pixel is assigned a habitat type from the Ontario Land Cover v1.0 data product. The pixels are combined into 300 m x 300 m pixels to correspond to other data sources. (See the Data Layers document for details on how the small pixels are combined, or resampled, into larger pixels). Pixels are classified further as degraded land, according to user-defined criteria. If pixels are classified as degraded, they are assigned a biodiversity value of zero in the tool. However, degraded pixels can be restored to a habitat that contributes to biodiversity. In the tool, degraded land is restored to the most prevalent habitat type in a 3 x 3-pixel neighbourhood (8 pixels in total) surrounding the degraded pixel. If a degraded pixel is not surrounded by any natural habitat in the 3 x 3 neighborhood, which may occur when the degraded land is surrounded by water, urban areas, or farmland, the degraded pixel is assigned the most prevalent habitat in successively larger neighborhoods that increase by 2 pixels each time (i.e., 5 x 5, 7 x 7, 9 x 9 neighbourhoods, etc.).

Not all habitat types are considered restorable. Pixels classified as water, built up-pervious, anthropogenic, cropland, hay/pastureland, and transportation are removed from the analysis. They are neither considered habitat with biodiversity benefit nor degraded land restorable to habitat with biodiversity benefit.

The user has two options for determining the size and configuration of candidate areas for restoration. First, they may define the number of pixels to restore regardless of where they are in the landscape or their potential habitat type. Second, the user may choose to restore only contiguous habitat (of any type). In this case, degraded pixels that all connect to each other and share the same habitat type are grouped into one multi-pixel degraded area. The pixels are considered connected if at least one corner from one pixel connects to a corner from another pixel. In the contiguous habitat area option, it is assumed that all pixels in the area are restored, irrespective of the size of the contiguous area.

Where does restoration take place?

Restoring with an emphasis on the entire landscape

Within this option, the user selects a landscape, and all pixels within that landscape will be considered for restoration. The user may select a landscape by drawing an extent manually, or by choosing from predefined features within land use designation layers. These features fall into multiple categories, one being municipalities. In Ontario, the Municipal Act defines two administrative scales: upper-tier municipalities comprised of lower-tier municipalities. Single-tier municipalities do not group into upper-tier municipalities, nor do they comprise lower-tier municipalities. The user can select to restore within upper/single-tier municipalities or lower-tier municipalities. Another category are areas of conservation concern that includes: Provincial Parks, National Parks, Conservation Reserves, Conservation Areas, Non-governmental Organization Reserves, Natural Heritage Value Areas, Natural Heritage System Areas, Far North Protected Areas, Municipal Heritage Areas, Migratory Bird Sanctuaries, National Wildlife Areas, Wilderness Areas, Crown Plan Protected Areas, Provincial Planned Protected Areas, National Capital Valued Ecosystem, Other Effective Area-based Conservation Measures.

Restoring with an emphasis on areas of conservation concern

Within this option, restoration benefit considers explicitly the benefit to an area of conservation concern. Calculating biodiversity benefit takes into account whether restoration increases the amount of habitat within an area of conservation concern and increases connectivity among multiple areas of conservation concern.

After setting the landscape within which restoration takes place, the user can add a buffer around the landscape. Doing so recognizes that restoring a pixel near or at a landscape border may increase patch size or connectivity at larger extents. Hence restoring an area may benefit the chosen landscape by enhancing biodiversity within the buffer surrounding the landscape.

What is biodiversity benefit?

Restoration benefits socio-ecological systems in numerous ways including conserving habitat for species-at-risk (Dickie et al. 2023), providing corridors for

organisms on the move (Brennan et al. 2022, Pither et al. 2023), mitigating against climate change (Timpane-Padgham et al. 2017), adding to protected area networks (Mappin et al. 2019), and enhancing the amount of carbon that can be stored as biomass (Strassburg et al. 2020, Currie et al. 2023). Designing a tool to address multiple benefits could require an unwieldy number of metrics that would be a challenge to compare and balance across a region as large as Ontario. A more tractable approach is to limit the scope of what restoration purports to benefit; the RestoratiON tool focuses solely on increasing biodiversity. It is species agnostic; it does not use data on species occurrences or abundances to measure how best to benefit a specific taxon (*sensu* Currie et al. 2023). Instead, the tool is informed by a half-century of research in community ecology, landscape ecology, and biogeography to predict potential biodiversity benefit based on where in a landscape restoration takes place.

In a landscape comprised of heterogeneous environmental conditions that can be organized into patches of different habitat types, biodiversity can be measured at different scales, and increasing biodiversity at one scale may reduce biodiversity at another. There can be a tension between increasing biodiversity in a patch, i.e., the smallest resolution at which environmental data is available and increasing biodiversity across the whole of the landscape. The tool takes as a starting point that each species has its optimal performance – and, thus, maximum population growth rate – in a specific set of environmental conditions (Thompson et al. 2020). As a result, any given environment will consist of a species hierarchy, with the species having the highest population growth rates able to compete better for resources than all other species. All else being equal, biodiversity across the landscape can be maximized by conserving as many different environments as possible (Fahrig et al. 2022). However, a suite of processes can ensure that dominant and subdominant species co-exist despite differences in competitive ability, some related to each species' fit to the environment (selection) and others related to random variation in demography (drift) and dispersal (Vellend 2010, Chase et al. 2020b). To reflect the interplay of the processes in shaping biodiversity across scales, the tool uses three metrics that each map onto selection, drift, and dispersal. The user can assign different weights to each metric to explore assumptions about the relative influence of each process on species coexistence.

Environmental heterogeneity

Species are described by their ecological niche: the range of environmental conditions over which an individual has positive fitness, or a population has positive growth (Hutchinson 1957, Holt 2009). At any given point in niche space, some species are more efficient at converting resources into reproduction and survival, resulting in a competitive hierarchy (Chesson 2000). Thus, even if a species can physiologically tolerate an environment, it may be outcompeted to the point of being excluded from that environment (Connell 1961, Martin and Ghalambor 2023). Restoration may add a new set of environmental conditions to the landscape that falls within the niche of species that could not previously occupy the area or provide opportunities for a species to avoid competition by exploiting newly available resources or habitats (Schoener 1974, Chesson 2000, Tews et al. 2004, Stein et al. 2014). While a niche consists of an infinite number of environmental conditions (Hutchinson 1957, Blonder 2018) the Restoration tool, necessarily, uses a reduced set of abiotic variables to describe the environment: temperature, precipitation, elevation, soil type, and soil depth. The variables are known to be correlated to species diversity and distributions (Hawkins et al. 2003, Gilbert and Lechowicz 2004, Opedal et al. 2015, Ayebare et al. 2023). The RestoratiON tool uses a Principal Components Analysis to assign each pixel a score that reflects the combination of these five environmental variables. Environmental heterogeneity measures the range of scores available in the landscape by calculating the deviation in pixel scores from the landscape average (Smith et al. 2021); heterogeneity increases if the deviation increases. The analysis calculates scores on multiple axes of variation, and the change in the deviation can be calculated for each dimension, though usually one or two dimensions are enough to capture environmental differences among pixels. For each candidate area, as pixels are restored, the tool determines if environmental heterogeneity increases or decreases. Increasing environmental heterogeneity increases regional diversity by supplying new niches exploitable by species that may previously have been excluded from the landscape. Increasing environmental heterogeneity may also increase local diversity if individuals exploiting new niches emigrate to patches corresponding to other environmental conditions.

Patch size

Some features of the environment vary at scales smaller than the pixel resolution. For example, a pixel classified as deciduous forest does not indicate the number of tree species in the forest or whether there is variation in canopy height. In such cases patch size becomes a surrogate for fine-scale environmental heterogeneity. Increasing patch size increases the chance that there are more kinds of fine-scale environments, such as more tree species or greater variation in canopy heights (Haila 1983, Dunning et al. 1992, Kallimanis et al. 2008). The increase in fine-scale environmental heterogeneity can offset the effects of competition by providing new niches (Silvertown 2004, Lasky et al. 2014). Increasing patch size also increases local biodiversity by mitigating extinction from stochastic events, such as drift and random environmental fluctuations, a risk that is greater for smaller populations (Orrock and Watling 2010, Gilbert and Levine 2017). Larger patches tend to support larger population sizes by providing more physical space and incorporating more individuals from the landscape (Wright 1983) and/or by fostering higher demographic rates (Chase et al. 2020a). However, when restoration resources are limited, the gain in local biodiversity by adding habitat to existing patches must be traded-off with increasing regional diversity by restoring patches that are more environmentally distinct but smaller (Margules and Pressey 2000, Fahrig et al. 2022, Riva and Fahrig 2022, 2023).

Connectivity

If restoration facilitates the movement and dispersal of individuals, then there is the potential to increase biodiversity both locally and for the landscape. Immigration of individuals into habitat patches can increase population sizes, reducing extinction risk (Pulliam 1988, Hanski 1998). Likewise, individuals produced in optimal environments can colonize, establish, and maintain stable populations in suboptimal environments (Leibold et al. 2004). Hence connectivity can increase local biodiversity. Connectivity can increase regional diversity if environmental conditions change slowly over broad gradients because individuals may only be able to disperse over short distances, leading to a landscape consisting of connected patches grouped into unconnected subregions each with a distinct species assemblage (Thompson et al. 2020, Suzuki and Economo 2021). In contrast, connectivity can decrease regional diversity if species can disperse everywhere. The entire landscape functions as one large patch and the species

adapted to the average environmental conditions outcompete the species fit to the more extreme environments (Mouquet and Loreau 2003, Lasky and Keitt 2013). Just what it means for a landscape to be connected depends on the resistance organisms might face when having to move through inhospitable environments (McRae et al. 2008). In the RestoratiON tool, pixels are assigned a resistance value with low and high resistance corresponding to habitat and non-habitat pixels. In addition, if the Areas of Conservation Concern option was chosen, pixels classified as such are assigned an even lower resistance value. When habitat is restored, a pixel previously assigned high resistance (by virtue of being degraded) becomes low resistance, and connectivity increases when more low resistance paths connecting habitat pixels become available (Chubaty et al. 2020). Increasing connectivity may not always be a good thing.

How are restoration areas prioritized?

In the RestoratiON tool, users can explore how varying assumptions about the ecological processes that shape biodiversity affect the choice of degraded pixels to restore. The user can adjust the amount that each metric – environmental heterogeneity, patch size, and connectivity – contributes to overall biodiversity benefit. The user may assign more weight to environmental heterogeneity if the main process structuring communities is selection, and the goal is to maximize biodiversity in the landscape. In contrast, the user may wish to assign more weight to patch size if the main process is drift or if the goal is to maximize local biodiversity. If a landscape is comprised of diverse environments, assigning more weight to environmental heterogeneity may ensure the persistence of species with distinct niches. On the other hand, if most species can occupy the range of environmental conditions in a landscape, but only when fine-scale heterogeneity mitigates against competitive exclusion, then more weight should be assigned to patch size. Different weights can be assigned to patches of different land cover types if, for example, known habitat specialists are more likely to persist if cover of that particular habitat is increased. Connectivity is usually important but could be downweighed if high rates of dispersal reduce diversity by excluding species with low abundances. On the other hand, connectivity might be prioritized for landscapes home to many vagile species or species that require different kinds of environments during their lifetime.

References

- Ayebare, S., J. W. Doser, A. J. Plumptre, I. Owiunji, H. Mugabe, and E. F. Zipkin. 2023. An environmental habitat gradient and within-habitat segregation enable co-existence of ecologically similar bird species. Proceedings of the Royal Society B: Biological Sciences 290:20230467.
- Blonder, B. 2018. Hypervolume concepts in niche- and trait-based ecology. Ecography 41:1441–1455.
- Brennan, A., R. Naidoo, L. Greenstreet, Z. Mehrabi, N. Ramankutty, and C. Kremen. 2022. Functional connectivity of the world's protected areas. Science 376:1101–1104.
- Chase, J. M., S. A. Blowes, T. M. Knight, K. Gerstner, and F. May. 2020a. Ecosystem decay exacerbates biodiversity loss with habitat loss. Nature 584:238–243.
- Chase, J. M., A. Jeliazkov, E. Ladouceur, and D. S. Viana. 2020b. Biodiversity conservation through the lens of metacommunity ecology. Annals of the New York Academy of Sciences 1469:86–104.
- Chesson, P. 2000. Mechanisms of Maintenance of Species Diversity. Annual Review of Ecology, Evolution, and Systematics 31:343–66.
- Chubaty, A. M., P. Galpern, and S. C. Doctolero. 2020. The R toolbox GRAINSCAPE for modelling and visualizing landscape connectivity using spatially explicit networks. Methods in Ecology and Evolution 11:591–595.
- Connell, J. H. 1961. The Influence of Interspecific Competition and Other Factors on the Distribution of the Barnacle Chthamalus Stellatus. Ecology 42:710–710.
- Currie, J., W. Merritt, C. Liang, C. Sothe, C. R. Beatty, N. Shackelford, K. Hirsh-Pearson, A. Gonsamo, and J. Snider. 2023. Prioritizing ecological restoration of converted lands in Canada by spatially integrating organic carbon storage and biodiversity benefits. Conservation Science and Practice:e12924.
- Dickie, M., C. Bampfylde, T. J. Habib, M. Cody, K. Benesh, M. Kellner, M. McLellan, S. Boutin, and R. Serrouya. 2023. Where to begin? A flexible framework to prioritize caribou habitat restoration. Restoration Ecology 31:e13873.
- Dunning, J. B., B. J. Danielson, and H. R. Pulliam. 1992. Ecological Processes That Affect Populations in Complex Landscapes. Oikos 65:169.
- Fahrig, L., J. I. Watling, C. A. Arnillas, V. Arroyo-Rodríguez, T. Jörger-Hickfang, J. Müller, H. M. Pereira, F. Riva, V. Rösch, S. Seibold, T. Tscharntke, and F.

May. 2022. Resolving the SLOSS dilemma for biodiversity conservation: a research agenda. Biological Reviews 97:99–114.

- Gilbert, B., and M. J. Lechowicz. 2004. Neutrality, niches, and dispersal in a temperate forest understory. Proceedings of the National Academy of Sciences 101:7651–7656.
- Haila, Y. 1983. Colonization of islands in a north-boreal Finnish lake by land birds. Annales Zoologici Fennici 20:179–197.
- Hawkins, B. A., R. Field, H. V. Cornell, D. J. Currie, J.-F. Guégan, D. M. Kaufman, J. T. Kerr, G. G. Mittelbach, T. Oberdorff, E. M. O'Brien, E. E. Porter, and J. R. G. Turner. 2003. Energy, water, and broad-scale geographic patterns of species richness. Ecology 84:3105–3117.
- Hirsh-Pearson, K., C. J. Johnson, R. Schuster, R. D. Wheate, and O. Venter. 2022. Canada's human footprint reveals large intact areas juxtaposed against areas under immense anthropogenic pressure. FACETS 7:398–419.
- Holt, R. D. 2009. Bringing the Hutchinsonian niche into the 21st century: ecological and evolutionary perspectives. Proceedings of the National Academy of Sciences of the United States of America 106 Suppl:19659–19665.
- Hutchinson, G. E. 1957. Concluding remarks. Cold Spring Harbor Symposia on Quantitative Biology 22:415–427.
- Kallimanis, A. S., A. D. Mazaris, J. Tzanopoulos, J. M. Halley, J. D. Pantis, and S. P. Sgardelis. 2008. How does habitat diversity affect the species–area relationship? Global Ecology and Biogeography 17:532–538.
- Lasky, J. R., and T. H. Keitt. 2013. Reserve Size and Fragmentation Alter Community Assembly, Diversity, and Dynamics. The American Naturalist 182:E142–E160.
- Lasky, J. R., M. Uriarte, V. K. Boukili, and R. L. Chazdon. 2014. Trait-mediated assembly processes predict successional changes in community diversity of tropical forests. Proceedings of the National Academy of Sciences 111:5616–5621.
- Mappin, B., A. L. M. Chauvenet, V. M. Adams, M. Di Marco, H. L. Beyer, O. Venter, B. S. Halpern, H. P. Possingham, and J. E. M. Watson. 2019.
 Restoration priorities to achieve the global protected area target. Conservation Letters 12:e12646.
- Margules, C. R., and R. L. Pressey. 2000. Systematic conservation planning. Nature 405:243–253.
- Martin, P. R., and C. K. Ghalambor. 2023. A Case for the "Competitive Exclusion–Tolerance Rule" as a General Cause of Species Turnover along Environmental Gradients. The American Naturalist 202:1–17.

- McRae, B. H., B. G. Dickson, T. H. Keitt, and V. B. Shah. 2008. Using circuit theory to model connectivity in ecology, evolution, and conservation. Ecology 89:2712–2724.
- Mouquet, N., and M. Loreau. 2003. Community Patterns in Source-Sink Metacommunities. The American Naturalist 162:544–557.
- Opedal, Ø. H., W. S. Armbruster, and B. J. Graae. 2015. Linking small-scale topography with microclimate, plant species diversity and intra-specific trait variation in an alpine landscape. Plant Ecology & Diversity 8:305–315.
- Pither, R., P. O'Brien, A. Brennan, K. Hirsh-Pearson, and J. Bowman. 2023. Predicting areas important for ecological connectivity throughout Canada. PLOS ONE 18:e0281980.
- Riva, F., and L. Fahrig. 2022. Landscape-scale habitat fragmentation is positively related to biodiversity, despite patch-scale ecosystem decay. Ecology Letters:ele.14145.
- Riva, F., and L. Fahrig. 2023. Obstruction of biodiversity conservation by minimum patch size criteria. Conservation Biology:e14092.
- Schoener, T. W. 1974. Resource partitioning in ecological communities. Science 185:27–39.
- Silvertown, J. 2004. Plant coexistence and the niche. Trends in Ecology and Evolution 19:605–611.
- Smith, A. C., K. M. Dahlin, S. Record, J. K. Costanza, A. M. Wilson, and P. L. Zarnetske. 2021. The GEODIV R package: Tools for calculating gradient surface metrics. Methods in Ecology and Evolution 12:2094–2100.
- Stein, A., K. Gerstner, and H. Kreft. 2014. Environmental heterogeneity as a universal driver of species richness across taxa, biomes and spatial scales. Ecology Letters 17:866–880.
- Strassburg, B. B. N., A. Iribarrem, H. L. Beyer, C. L. Cordeiro, R. Crouzeilles, C. C. Jakovac, A. Braga Junqueira, E. Lacerda, A. E. Latawiec, A. Balmford, T. M. Brooks, S. H. M. Butchart, R. L. Chazdon, K.-H. Erb, P. Brancalion, G. Buchanan, D. Cooper, S. Díaz, P. F. Donald, V. Kapos, D. Leclère, L. Miles, M. Obersteiner, C. Plutzar, C. A. de M. Scaramuzza, F. R. Scarano, and P. Visconti. 2020. Global priority areas for ecosystem restoration. Nature 586:724–729.
- Suzuki, Y., and E. P. Economo. 2021. From species sorting to mass effects: spatial network structure mediates the shift between metacommunity archetypes. Ecography 44:715–726.
- Tews, J., U. Brose, V. Grimm, K. Tielbörger, M. C. Wichmann, M. Schwager, and F. Jeltsch. 2004. Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. Journal of Biogeography 31:79–92.

- Thompson, P. L., L. Melissa Guzman, L. De Meester, Z. Horváth, R. Ptacnik, B. Vanschoenwinkel, D. S. Viana, and J. M. Chase. 2020. A process-based metacommunity framework linking local and regional scale community ecology. Ecology Letters 23:1314–1329.
- Timpane-Padgham, B. L., T. Beechie, and T. Klinger. 2017. A systematic review of ecological attributes that confer resilience to climate change in environmental restoration. PLOS ONE 12:e0173812.
- Vellend, M. 2010. Conceptual synthesis in community ecology. The Quarterly review of biology 85:183–206.
- Wright, D. H. 1983. Species-energy theory: an extension of species-area theory. Oikos 41:496–506.