Optimizing conservation of migratory species over their full annual cycle in the Western Hemisphere

One-sentence summary: Area-based plans to conserve migratory birds of the Western Hemisphere over their full annual cycle revealed high compatibility between land use plans likely to support human livelihoods and conserve Neotropical migratory birds.

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Strategic plans to conserve migratory species require detailed knowledge on species distribution, abundance, and habitat use over the annual cycle, but such data are lacking for most species. We developed a hemispheric approach to planning using spatiotemporally explicit species abundance models to prioritize land needed to conserve ≥17% of the global populations of 109 species of Neotropical migratory birds. The efficiency of annual cycle plans was evaluated in comparisons to single-season plans, and to scenarios that avoided areas with a high human footprint index. Annual cycle plans were more efficient than single-season plans and reduced the area needed to meet 17% targets by up to 43%. Area efficiency was maximized when land converted by human activity (e.g., agricultural, urban) was included in solutions, suggesting that working landscapes contribute positively to conservation. Here we show that annual cycle plans and land-sharing approaches to conservation can help identify land use scenarios capable of supporting human livelihoods and Neotropical migratory birds.

Land-use change is the greatest global threat to biodiversity, ecosystems[1], and the services they provide[2,3], and migratory species are particularly vulnerable to such change given the vast geographic areas occupied over the annual cycle[4,5]. Strategic approaches to the conservation of migratory species are therefore required to identify and protect habitats critical to the persistence of all target species. However, substantial gaps in knowledge of the abundance, distribution, and demography of most migratory species[6] have hampered strategic planning and led to uncertainty about the optimal allocation of conservation effort[5,7]. Given that populations of many migratory species continue to decline[4,8], there is an urgent need to assemble and act on the best data available.

Multi-species decision support tools have the potential to facilitate dramatically the strategic identification of areas critical to the conservation of migratory species but have remained intractable due to limits on knowledge and computing power. We capitalized on advances in crowd-sourced models of bird species abundance and distribution[9,10] and linear programing[11] to develop a robust multi-species planning tool to estimate the land base needed to conserve 109 Nearctic-Neotropical migratory songbirds (Supplementary Table S1) during the spring and fall migration and stationary breeding and 'non-breeding' periods. Specifically, we combined fine-scale, predictive models of species distribution and abundance in each of four periods with spatial optimization tools[12] to estimate the amounts and types of land needed to conserve our focal species populations over their full annual cycles at a hemispheric scale.

We first modeled global populations of 109 migratory species in their migration, breeding and non-breeding ranges using spatiotemporal exploratory models to estimate relative abundance for each species (Fig. 1). We next created area optimized solutions to conserve 17% of the global populations of each species over the annual cycle, and then recorded land cover for each solution. This target derives from the UN Convention on Biological Diversity (CBD) Aichi Biodiversity Target 11, which aims to conserve 17% of terrestrial and fresh-water ecosystems, emphasizing areas with high biodiversity. We also compared the geographic areas selected when optimizing the migration, breeding and non-breeding periods separately to the areas selected when the seasons were optimized simultaneously over the annual cycle. Because existing plans consider breeding and non-breeding periods separately[13,14], our analysis offers the first example of spatial optimization that considers the full annual cycle.

Finally, we compared area-based conservation plans that represent two different perspectives on the value of human-modified landscapes for the conservation of migratory birds.

Our ‘land-sparing’ approach emphasized the protection of relatively intact habitat as indicated by a low human footprint index[15] (Fig. S1), whereas our ‘land sharing’ approach was more permissive to human activities[16].

Results

We found that area-efficiency of conservation improved greatly when land was prioritized over the full annual cycle, rather than separately by season. We found a 43% (2.01M km^2) reduction in the area needed to meet the target given a land-sharing scenario (Fig. 2), and a 27% (1.8M km^2) reduction in the area needed given land-sparing (Fig. 3; Table 1).

Higher efficiency in full annual cycle plans is achieved by identifying sites that contribute to species’ population targets in more than one season. These overlapping sites can contribute to the targets for a single species (e.g. a species uses a site for breeding and migration) or multiple species (e.g. one species uses a site for breeding while another uses it for migration). The resulting efficiency suggests there may be value in reviewing how conservation investments are allocated at large spatial scales. Currently, government and non-governmental organizations allocate up to $1 billion annually to bird conservation based on aspatial targets and expert elicitation, with most actions aimed at the conservation of breeding habitat[13,14]. In contrast, our results suggest that wherever possible, conservation investments for migratory species should be based on assessments over the annual cycle[5,7,10].

Our results also indicate that conserving land in human-dominated, working landscapes may be part of an efficient strategy to conserve Neotropical migratory birds. A land-sharing approach required 45% less land area than land-sparing when planning over the annual cycle, and 31% less land area than land-sparing when planning over single seasons (Table 1). However,

these gains in efficiency were distributed unequally across seasons. Land sharing returned the largest gains in efficiency in the stationary non-breeding, fall and spring migration periods, reducing area reserved by 1.24M km^2 (55.4%), 1.67M km^2 (49.4%), and 1.85M km^2 (55.2%) respectively, compared to a reduction of 0.91M km^2 (30.4%) in the breeding period (Table 1). This suggests that regions of Latin America and the Caribbean may be where conservation investments can most efficiently conserve habitat in working landscapes that sustain human livelihoods and Neotropical migratory birds[17].

Land-sparing and sharing solutions also varied geographically and by ecosystem type. Land-sparing approaches selected larger areas of needle-leaved forest in boreal and mountainous zones of western Canada, and more broad-leaved evergreen forest in the eastern Andes and western Amazon basin (Fig. 4; Table 2). Single-season and full annual cycle approaches to land-sparing resulted in geographically similar outcomes (Table 2; Fig. 3). In contrast, annual cycle plans using land-sharing reduced the area of mixed coniferous-deciduous forests reserved by 59% but increased the area of broadleaf evergreen forest by 2%. The area of needle-leaf evergreen forest and herbaceous-grassland identified also declined given land-sharing (53% and 50% reductions, respectively), indicating that full annual cycle approaches reduced plan area by ≥27% for all but one land cover type (broadleaf evergreen; Table 2).

Land-sharing scenarios included more urban land than expected given the extents of all cover types, but relatively little overall (2.9% of optimized annual cycle plan; Table 2). Although urban expansion threatens many species[18], some urban areas support relatively diverse species pools[19] and threatened species[20]. Recent studies on Neotropical migrants have shown how this group appears to use urban sites more often than expected during migration[6,21].

Despite higher efficiency in land-sharing versus sparing approaches, several caveats exist. First, these two approaches are not mutually exclusive; effective conservation will require both given that some migratory and many resident species cannot be conserved in working landscapes[22]. Second, implementing conservation within working landscapes may be more challenging than in areas with less human activity. Third, areas used by humans and selected in land-sharing scenarios may degrade in habitat value over time via agricultural intensification or urbanization[23]. Insuring that working landscapes support Neotropical migrants in future may therefore require incentives to encourage practices that conserve or enhance habitat values for birds and also sustain human well-being. Fourth, the 17% target adopted here is illustrative only; larger targets will be needed to avoid range contraction and local extinction, and to conserve ecological functions, such as seed dispersal and pest control[24]. Nevertheless, 17% exceeds the areal extent of conservation plans that currently exist in support of Neotropical migrant birds. Last, our approach did not consider migratory connectivity[25] because all approaches selected sites that met targets for each species anywhere within their range. In contrast, for species that show strong connectivity between the breeding and stationary non-breeding ranges, or if different populations use different migratory pathways, our analysis will over-represent a 17% target in some parts of the species' range and under-represent it in others. As tracking technologies improve, migratory connectivity could be incorporated explicitly into planning tools, or methods could be applied to insure spatial representation. However, because it could take decades to describe migratory connectivity in all 109 species used here, we suggest that our approach to annual cycle planning represents a precautionary, first step to developing hemispheric-scale plans for the conservation of Neotropical migratory birds[26].

Discussion

Ongoing declines and range constrictions in migratory species and severe limits on financial and human resources[27] point to an urgent need for area-based plans that maximize the efficiency of conservation investments while minimizing opportunity costs[28]. We explored solutions optimized on area-efficiency and suggest two key lessons. First, scenarios that considered all habitats used over the annual cycle were more efficient than those which considered the migration, breeding and non-breeding periods separately. Second, area-based plans that accommodated human activity, represent a land-sharing approach to conservation, were more efficient than land-sparing approaches which avoided areas with a high human footprint. In addition, although we focused on Neotropical migrant birds, our approach could be replicated for migratory species and systems given sufficient spatial data. In our case, citizen science data and advanced prioritization tools allowed us to reveal efficiencies in area-based plans spanning multiple seasons and jurisdictions. We further showed that land-sharing scenarios that included working landscapes increased area-efficiency, indicating that incentives to avoid agricultural intensification may be required to ensure that these efficiencies are retained. The high concentration of migratory birds and land required to support them in the non-breeding period further emphasizes that investments in Latin America and the Caribbean currently represent the most efficient way to conserve Neotropical migrant birds.

Methods

Species selection

We initially considered 118 species of Neotropical migratory passerines for our analysis (Extended Data Table 1). These species fell into two broad groups based on their breeding and stationary non-breeding ranges: 1) species where individuals breed in North America north of the US-Mexico border and migrate south of the Tropic of Cancer during the non-breeding period (n=101 species, Extended Data Table 1), 2) species with migratory and resident populations or subspecies; individuals from migratory populations north of the US-Mexico border move south of the Tropic of Cancer during the non-breeding period (n=17 species). We then removed 9 species because there was insufficient data to identify their stationary non-breeding range (see Extended Data Table 1). These were primarily species that overwinter in parts of South America with limited eBird coverage or where identification is problematic during the non-breeding season (e.g. alder and willow flycatcher). The remaining 109 species were included in the final analysis.

Spatial prioritization approach

Here we use the concept of systematic conservation planning[29], to inform choices about areas to protect, in order to optimize outcomes for biodiversity while minimizing societal costs[30]. To achieve the goal to optimize the trade-off between conservation benefit and socioeconomic cost, i.e. to get the most benefit for limited conservation funds, we strive to minimize an objective function over a set of decision variables, subject to a series of constraints. Integer linear programming (ILP) is the subset of optimization algorithms used here to solve reserve design problems. The general form of an ILP problem can be expressed in matrix notation as:

$$Minimize\ c^T x\ subject\ to\ Ax\ \geq\ b$$

Where x is a vector of decision variables, c and b are vectors of known coefficients, and A is the constraint matrix. The final term specifies a series of structural constraints where relational operators for the constraint can be either ≥ the coefficients. In the minimum set cover problem, c is a vector of costs for each planning unit, b a vector of targets for each conservation feature, the relational operator would be ≥ for all features, and A is the representation matrix with Aij=rij, the representation level of feature i in planning unit j. We set an objective to find the solution that fulfills all the targets and constraints for the smallest cost[11]. This objective is similar to that used in Marxan, the widest used software for spatial conservation planning to date[31].

Spatiotemporal exploratory models

We used spatiotemporal exploratory models (STEM)[9,32,33] to generate estimates of relative abundance for each species. STEM is an ensemble of local regression models generated from a spatiotemporal block subsampling design. Repeatedly subsampling and partitioning the study extent into grids of spatiotemporal blocks, and then fitting independent regression models (base models) in each block produces an ensemble of partially overlapping local models. Estimates at a given location and date are made by averaging across all the local models that contain the location and date. Combining estimates across the ensemble controls for inter-model variability[34] and adapts to non-stationary predictor–response relationships[32]. To account for spatial variation in the density of the bird observation data[35], smaller spatiotemporal blocks (10° × 10° × 30 continuous days) were used north of 12° latitude and larger blocks (20° × 20° × 30 continuous days) were used in the southern portion of the study extent.

The bird observation data used to implement STEM came from the eBird citizen-science database[36]. The data included species counts from complete checklists collected under the "traveling", "stationary", and "areal" protocols from January 1, 2004 to December 31, 2016 within the spatial extent bounded by 180° to 30° W Longitude (as well as Alaska between 150° E and 180° E). This resulted in a dataset consisting of 14 million checklists collected at 1.7 million unique locations, of which 10% were withheld for model validation.

Within each base model, species' occupancy and abundance was assumed to be stationary. We fit zero-inflated boosted regression trees[9] to predict the observed counts (abundance) of species based on three general classes of predictors: i) spatial predictors to account for spatial (and spatiotemporal) patterns; ii) temporal predictors to account for trends; and iii) predictors that describe the observation/detection process, which account for variation in detection rates, a nuisance when making inference about species occupancy and abundance. Spatial information was captured using elevation[37] and NASA MODIS land[38] and water cover data. The MODIS data were summarized as the proportion and spatial configuration of each of the 19 cover classes within 2.8 × 2.8 km (784 hectare) pixels centered at each eBird location using FRAGSTATS[39] and SDMTools[40]. Summarizing the land-cover information at this resolution reduced the impact of erroneous cover classifications, and reduced the impact of inaccurate eBird checklist locations. The time of day was used to model variation in availability for detection; e.g., diurnal variation in behavior, such as participation in the "dawn chorus"[41]. Day of the year (1-366) was used to capture day-to-day changes in occupancy, and year was included to account for year-to-year differences. Finally, to account for variation in detection rates variables for the number of hours spent searching for species, the length of the transect

traveled during the search, and the number of people in the search party were included in each base model.

Estimates of relative abundance and occupancy were rendered at weekly temporal resolution and 8.4 × 8.4 km spatial resolution. Each estimate was calculated as an ensemble average across 50-100 base models. The quantity estimated was either the expected number of birds of a given species (abundance) or the probability of the species being reported (occupancy) by a typical eBird participant on a search starting from the center of the pixel from 7:00 to 8:00 AM while traveling 1 km.

Land use constraints

We used a total of two constraint metrics in the systematic conservation prioritization analysis. First, to avoid any restrictions on the species informed selection outcomes we used a constant cost metric, where each planning unit was assigned a cost value of 1. Second, we used the human footprint metric for 2009[15], which is available at a roughly 1 km spatial resolution, to select areas for conservation that have relatively low direct human pressures present. We calculated the mean human footprint value for each 8.4 x 8.4 km pixel throughout the study area, for use in the prioritization analysis.

Systematic conservation prioritization analysis

We combined the weekly estimates from the STEM models for each species into average breeding abundance estimates (June 6 – July 4) and non-breeding abundance estimates (December 26 – January 25). For the migration seasons we summed abundance estimates for each species up for spring (April 4 - May 2) and fall (August 8 - September 26). Each of the 109

species was treated as a feature in the prioritization analysis. We created scenarios for spring migration, breeding, fall migration, non-breeding and the combined time periods, while including either the unrestricted cost metric or the human footprint cost metric, to create a total of 10 scenarios. We used the prioritzr[42] R package for the analysis, which interfaces with the Gurobi[43] optimization software.

Land cover representation

After the prioritization analyses, we summarized the major land cover types for each scenario that we generated. We used the 2015 data set of the global land cover map[44] at a 300m resolution and clipped the original data to the study area. For each scenario, we used the geospatial data abstraction library[45] to warp the selected cells from the prioritization onto the raster grid of the land cover dataset. There were 37 land cover classes identified across scenarios and the frequency and area amount of each was summarized for all scenarios. As a final step we combined similar land cover classes into broader classes (Extended Data Table 2) and we used these to examine differences in area and land cover types selected under single season vs. full annual cycle planning and for land sparing vs land sharing scenarios (Table 2).

Code availability

All computer code used in analysis, files generated from the analysis and outputs such as figures and tables have been deposited and will be made publicly available on publication here: https://osf.io/58hgs/?view_only=4bddcf37b95e470da3d3d90ba0f260de. The STEM model outputs used as inputs to the analysis will be made publicly available shortly by the Cornell Lab of Ornithology.

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Extended Data (up to 10)

Extended Data Table 1| Bird species used in this analysis.

Extended Data Table 2| Individual and summarized land cover classes identified in this analysis.

Extended Data Figure 1| Human footprint estimated in 2009.

Acknowledgments: RS is supported by a Liber Ero Fellowship, ADR by a Garvin endowment, and JRB and PA by the Natural Sciences and Engineering Research Council of Canada. We also thank the eBird participants for their contributions and eBird team for their support. This work was funded by The Leon Levy Foundation, The Wolf Creek Charitable Foundation, NASA (NNH12ZDA001N-ECOF), Microsoft Azure Research Award (CRM: 0518680), and the National Science Foundation (ABI sustaining: DBI-1356308; computing support from CNS-1059284 and CCF-1522054). Data, analysis scripts and full results are archived here: https://osf.io/58hgs/?view_only=4bddcf37b95e470da3d3d90ba0f260de.

Author Contributions RS, SW, ADR, JRB and PA conceived the study. RS, DF and TA collected data and conducted analyses. All authors contributed to writing and editing the paper.

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Table 1: Area requirements to meet a 17% population target for 109 Neotropical migrant species under land sharing and land sparing scenarios. Each entry in the table shows the area required to meet the target (in million km^2). Values in brackets are the percent of the range selected to meet the target with total range sizes equaling 20.77M km^2 for the spring migration period, 24.68M km^2 on the breeding range, 26.67M km^2 for the fall migration period, 16.73M km^2 on the nonbreeding range and 31.62M km^2 for the combined breeding and non-breeding ranges. The final two columns show the total area amounts across all four seasons depending on whether the prioritization considers each season separately (single-season) or whether it minimizes areas across seasons where possible (full annual cycle).

Constraint	Migration Spring	Breeding	Migration Fall	Non-breeding	Single-season combined	Full annual cycle
Land sharing	1.5 (7.24)	2.08 (8.45)	1.71 (6.42)	1 (5.99)	4.75 (15.01)	2.73 (8.63)
Land sparing	3.35 (16.15)	2.99 (12.12)	3.38 (12.66)	2.24 (13.36)	6.72 (21.25)	4.92 (15.57)

Table 2. Area selected (1000 km^2) for major land cover types under single season and full annual cycle planning and for land sharing and sparing scenarios. Area available is the total amount of each land cover across the breeding and nonbreeding range based on cells where $\geq$ 1 species was present. % reduction is the percentage decrease in the area required for each land cover type with full annual cycle compared to single season planning. Not all land cover classes are included in the table and therefore individual land cover values do not sum to the total in each column. Land cover data was extracted from the global land cover map for 2015 (300m resolution)[44].

Land cover	**Area available**	**Land sharing**			**Land sparing**		
		Single season	Full annual cycle	% reduction	Single season	Full annual cycle	% reduction
Cropland/Mosaic Cropland	2269	252	149	41	201	162	19
Grassland	5555	1148	578	50	884	648	27
Urban areas	205	125	74	41	1	1	0
Broadleaf Deciduous Forest	1994	533	356	33	467	352	25
Broadleaf Evergreen Forest	6921	206	211	-2	1504	1197	20
Needleleaf Forest	4599	1076	509	53	1616	1133	30
Mixed Forest	966	277	114	59	317	211	33
Mosaic Forest	934	117	85	27	186	138	26
Flooded Forest	540	93	56	40	159	119	25
Shrubland	4226	516	318	38	731	493	33
Wetland	468	49	36	27	97	80	18
Barren	1053	56	36	36	199	127	36
Total	**31615**	**4746**	**2728**	**43**	**6904**	**4922**	**29**

Figure 1: Bird species diversity of the four seasons of the year. a) Shannon diversity index of 109 species of Neotropical migratory birds during the spring migration season (April 4 - May 2); **b)** Shannon diversity index for the breeding season (June 6 – July 4); **c)** Shannon diversity index for the fall migration season (August 8 - September 26); **d)** Shannon diversity index for the non-breeding period (December 26 – January 25).

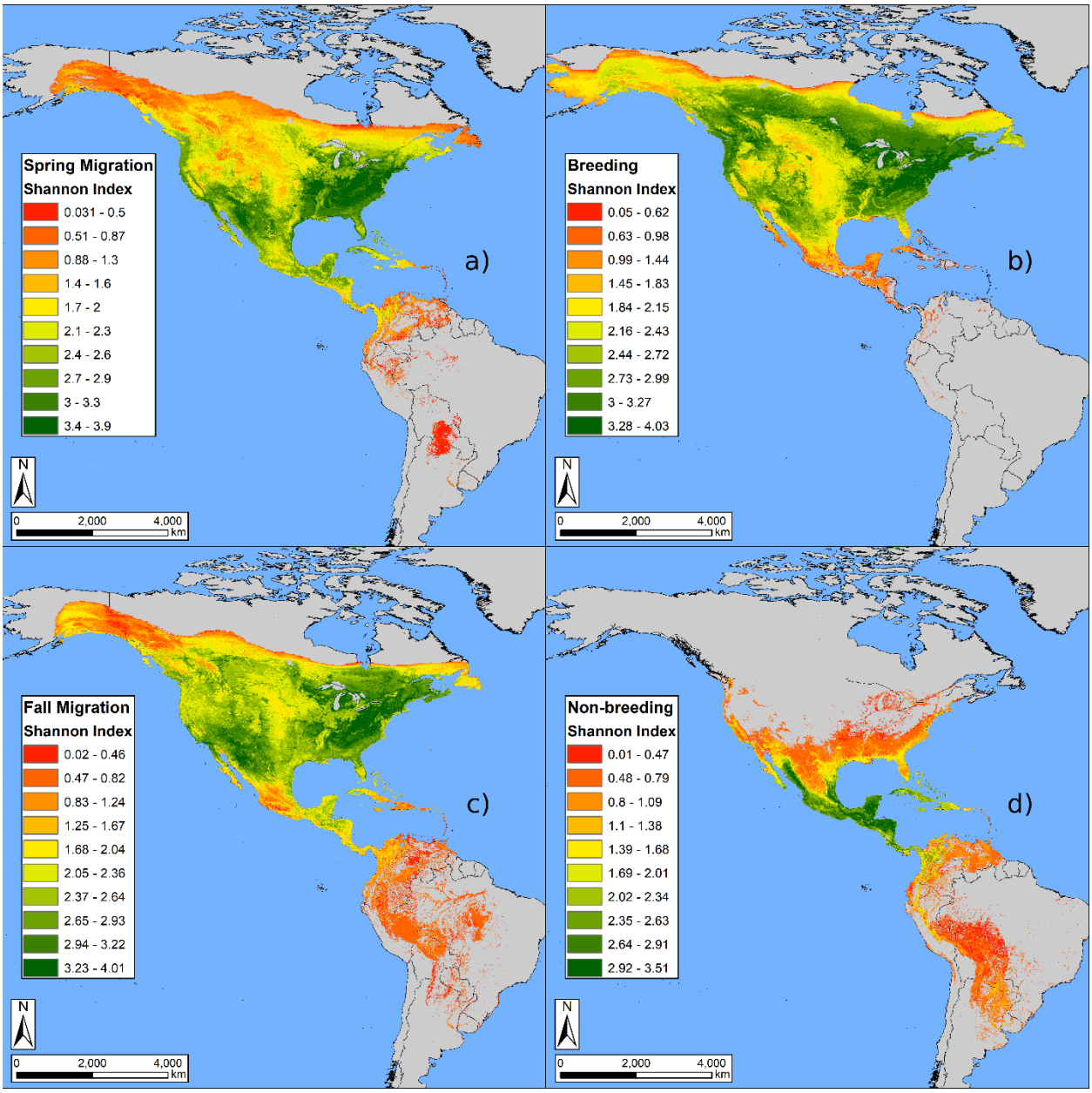


Figure 2. Comparison of areas prioritized for single season and full annual cycle planning under a land sharing approach allowing for the inclusion of human dominated landscapes. The prioritization is based on a target of 17% of global populations of 109 species of Neotropical migratory birds.

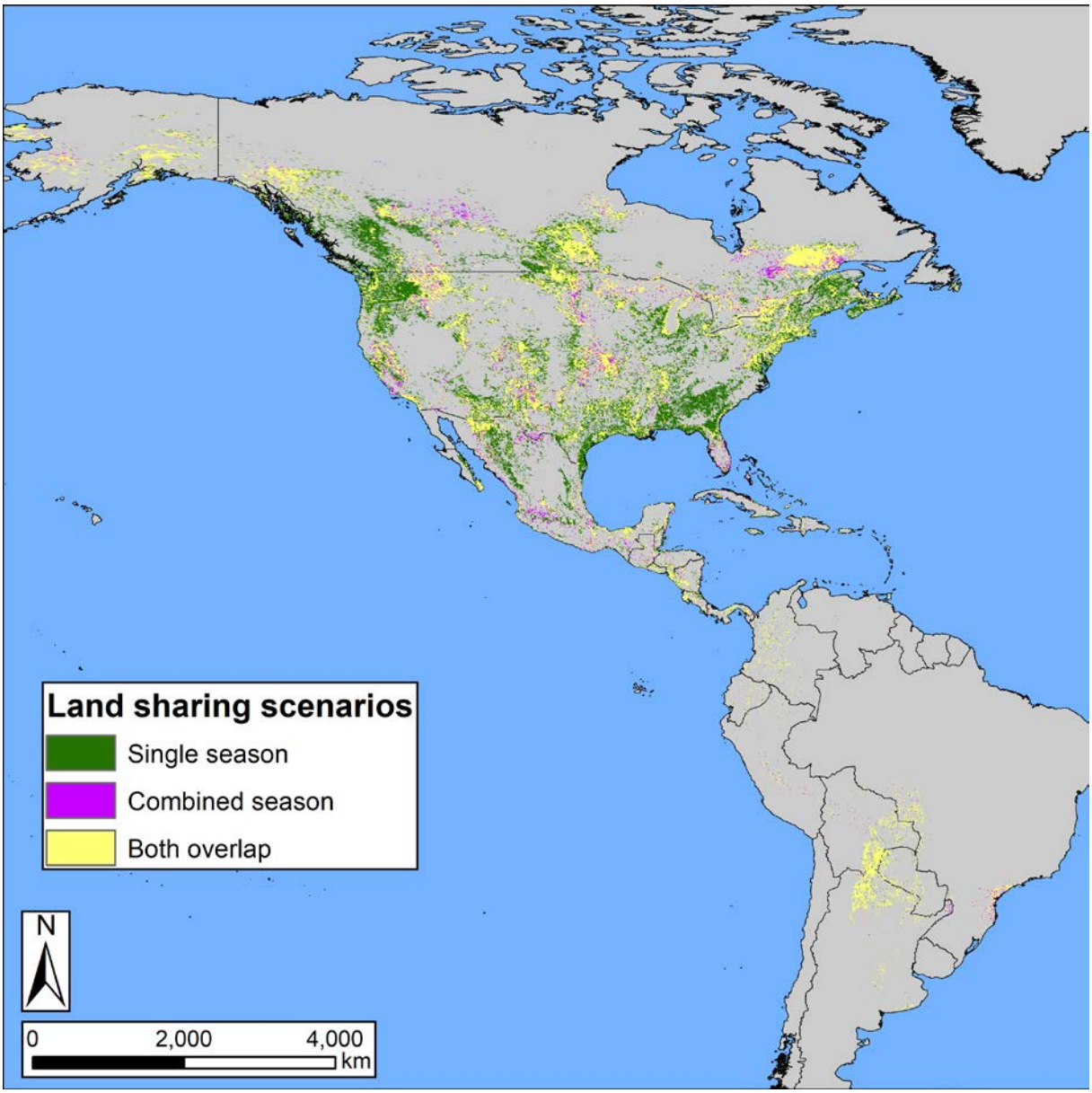


Figure 3. Comparison of areas prioritized for single season and full annual cycle planning under a land sparing approach that preferentially selects landscapes with a low human footprint. The prioritization is based on a target of 17% of global populations of 109 species of Neotropical migratory birds.

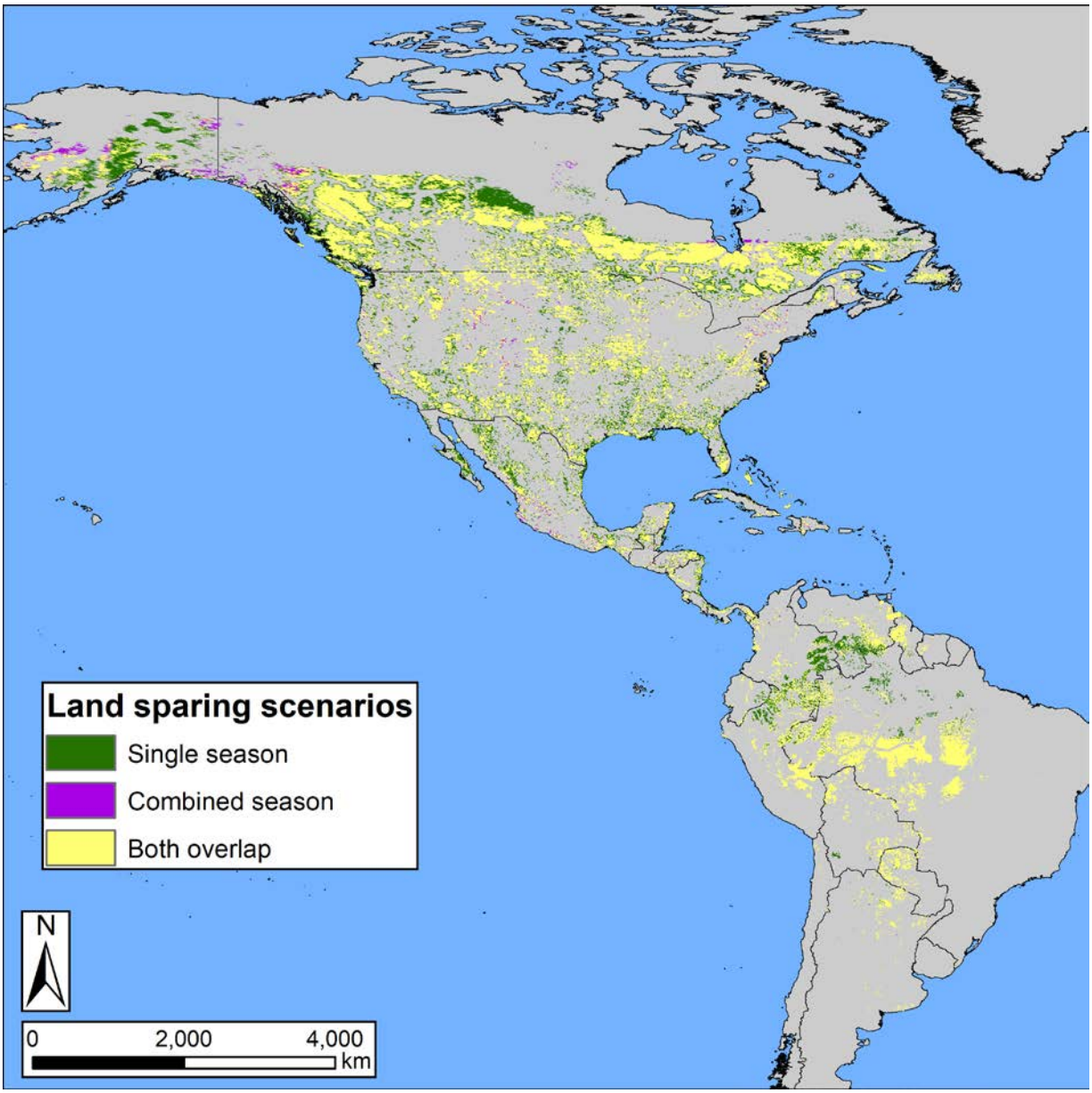
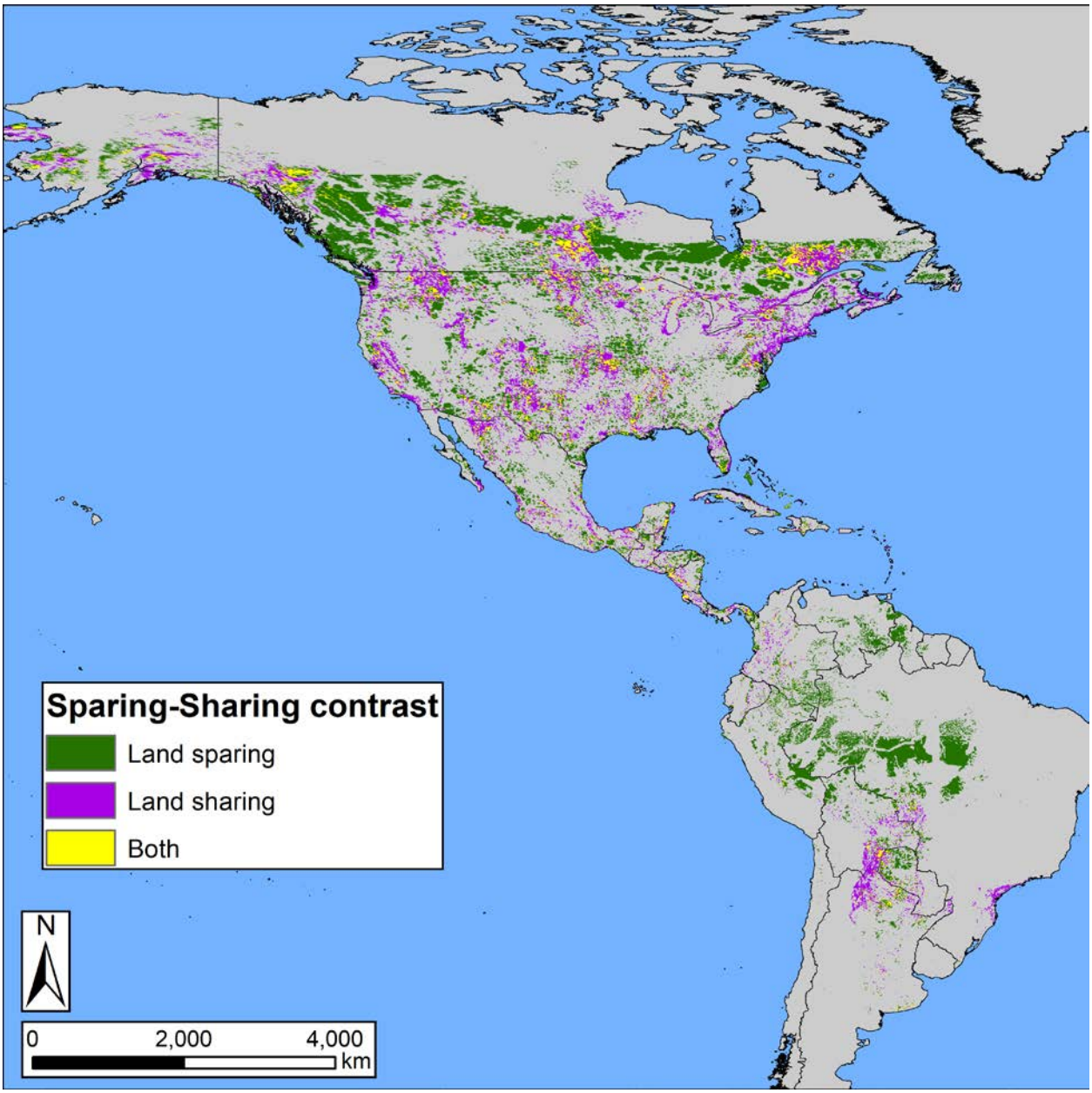


Figure 4: Land sharing and land sparing scenario comparison. Prioritized areas across the annual cycle, using a target of 17% of global populations of 109 species of Neotropical migratory birds. The land-sparing scenario used the Human Footprint Index[15] as a constraint, while the land-sharing scenario did not.



Extended Data Table 1. The 118 species of Neotropical migratory passerines considered for analysis and their range category. See Methods for range category descriptions. Species with an asterisk after the common name were left out of the analysis because of insufficient data for the stationary non-breeding range.

Common name	Scientific name	Range category
Acadian Flycatcher	*Empidonax virescens*	1
Alder Flycatcher*	*Empidonax alnorum*	1
American Redstart	*Setophaga ruticilla*	1
Ash-throated Flycatcher	*Myiarchus cinerascens*	1
Bay-breasted Warbler	*Setophaga castanea*	1
Baltimore Oriole	*Icterus galbula*	1
Bank Swallow	*Riparia riparia*	1
Barn Swallow	*Hirundo rustica*	2
Black-and-white Warbler	*Mniotilta varia*	1
Bell's Vireo	*Vireo bellii*	1
Black Swift*	*Cypseloides niger*	2
Blackburnian Warbler	*Setophaga fusca*	1
Black-billed Cuckoo*	*Coccyzus erythropthalmus*	1
Black-chinned Hummingbird	*Archilochus alexandri*	1
Black-capped Vireo	*Vireo atricapilla*	1
Black-headed Grosbeak	*Pheucticus melanocephalus*	2
Blackpoll Warbler	*Setophaga striata*	1
Blue Grosbeak	*Passerina caerulea*	2
Broad-tailed Hummingbird	*Selasphorus platycercus*	1
Black-throated Blue Warbler	*Setophaga caerulescens*	1
Black-throated Green Warbler	*Setophaga virens*	1
Black-throated Gray Warbler	*Setophaga nigrescens*	1
Blue-gray Gnatcatcher	*Polioptila caerulea*	2
Blue-headed Vireo	*Vireo solitarius*	1
Bullock's Oriole	*Icterus bullockii*	1
Blue-winged Warbler	*Vermivora cyanoptera*	1
Calliope Hummingbird	*Selasphorus calliope*	1
Cape May Warbler	*Setophaga tigrina*	1
Canada Warbler	*Cardellina canadensis*	1
Cassin's Kingbird	*Tyrannus vociferans*	2
Cassin's Vireo	*Vireo cassinii*	1
Cave Swallow	*Petrochelidon fulva*	2
Cerulean Warbler	*Setophaga cerulea*	1
Chestnut-sided Warbler	*Setophaga pensylvanica*	1
Chimney Swift*	*Chaetura pelagica*	1
Cliff Swallow	*Petrochelidon pyrrhonota*	1
Common Nighthawk*	*Chordeiles minor*	1
Common Yellowthroat	*Geothlypis trichas*	1
Connecticut Warbler*	*Oporornis agilis*	1

Cordilleran Flycatcher	*Empidonax occidentalis*	1
Dickcissel	*Spiza americana*	1
Dusky Flycatcher	*Empidonax oberholseri*	1
Eastern Kingbird	*Tyrannus tyrannus*	1
Eastern Wood-Pewee	*Contopus virens*	1
Golden-cheeked Warbler	*Setophaga chrysoparia*	1
Golden-winged Warbler	*Vermivora chrysoptera*	1
Grace's Warbler	*Setophaga graciae*	2
Great Crested Flycatcher	*Myiarchus crinitus*	1
Gray Catbird	*Dumetella carolinensis*	1
Gray Vireo	*Vireo vicinior*	1
Gray-cheeked Thrush	*Catharus minimus*	1
Hammond's Flycatcher	*Empidonax hammondii*	1
Hepatic Tanager	*Piranga flava*	2
Hermit Warbler	*Setophaga occidentalis*	1
Hooded Oriole	*Icterus cucullatus*	2
Hooded Warbler	*Setophaga citrina*	1
Indigo Bunting	*Passerina cyanea*	1
Kentucky Warbler	*Geothlypis formosa*	1
Lazuli Bunting	*Passerina amoena*	1
Least Flycatcher	*Empidonax minimus*	1
Louisiana Waterthrush	*Parkesia motacilla*	1
Lucy's Warbler	*Oreothlypis luciae*	1
MacGillivray's Warbler	*Geothlypis tolmiei*	1
Magnolia Warbler	*Setophaga magnolia*	1
Mourning Warbler	*Geothlypis philadelphia*	1
Nashville Warbler	*Oreothlypis ruficapilla*	1
Northern Parula	*Setophaga americana*	1
Northern Waterthrush	*Parkesia noveboracensis*	1
Northern Rough-winged Swallow	*Stelgidopteryx serripennis*	1
Olive-sided Flycatcher	*Contopus cooperi*	1
Orchard Oriole	*Icterus spurius*	1
Orange-crowned Warbler	*Oreothlypis celata*	1
Ovenbird	*Seiurus aurocapilla*	1
Painted Bunting	*Passerina ciris*	1
Painted Redstart	*Myioborus pictus*	2
Palm Warbler	*Setophaga palmarum*	1
Pacific-slope Flycatcher	*Empidonax difficilis*	1
Philadelphia Vireo	*Vireo philadelphicus*	1
Plumbeous Vireo	*Vireo plumbeus*	1
Prairie Warbler	*Setophaga discolor*	1
Prothonotary Warbler	*Protonotaria citrea*	1
Purple Martin	*Progne subis*	1
Red-eyed Vireo	*Vireo olivaceus*	2
Red-faced Warbler	*Cardellina rubrifrons*	2

Rose-breasted Grosbeak	*Pheucticus ludovicianus*	1
Ruby-throated Hummingbird	*Archilochus colubris*	1
Ruby-crowned Kinglet	*Regulus calendula*	1
Rufous Hummingbird	*Selasphorus rufus*	1
Scarlet Tanager	*Piranga olivacea*	1
Scott's Oriole	*Icterus parisorum*	2
Scissor-tailed Flycatcher	*Tyrannus forficatus*	1
Summer Tanager	*Piranga rubra*	1
Swainson's Thrush	*Catharus ustulatus*	1
Swainson's Warbler	*Limnothlypis swainsonii*	1
Tennessee Warbler	*Oreothlypis peregrina*	1
Townsend's Warbler	*Setophaga townsendi*	1
Tree Swallow	*Tachycineta bicolor*	1
Vaux's Swift	*Chaetura vauxi*	2
Veery*	*Catharus fuscescens*	1
Violet-green Swallow	*Tachycineta thalassina*	1
Virginia's Warbler	*Oreothlypis virginiae*	1
Warbling Vireo	*Vireo gilvus*	1
Western Kingbird	*Tyrannus verticalis*	1
Western Tanager	*Piranga ludoviciana*	1
Western Wood-Pewee	*Contopus sordidulus*	1
White-eyed Vireo	*Vireo griseus*	1
White-throated Swift	*Aeronautes saxatalis*	2
Willow Flycatcher*	*Empidonax traillii*	1
Wilson's Warbler	*Cardellina pusilla*	1
Worm-eating Warbler	*Helmitheros vermivorum*	1
Wood Thrush	*Hylocichla mustelina*	1
Yellow-breasted Chat	*Icteria virens*	1
Yellow-bellied Flycatcher	*Empidonax flaviventris*	1
Yellow-billed Cuckoo*	*Coccyzus americanus*	1
Yellow Warbler	*Setophaga petechia*	2
Yellow-rumped Warbler	*Setophaga coronata*	1
Yellow-throated Vireo	*Vireo flavifrons*	1
Yellow-throated Warbler	*Setophaga dominica*	1

Extended Data Table 2. Summarized and individual land cover classes used to examine selection of land cover types under single season vs. full annual cycle planning and for land sharing vs sparing scenarios. See ref. 44 for further descriptions of the individual land cover classes.

Summary class	**Individual classes**
Cropland/Mosaic Cropland	Cropland/rainfed
Cropland/Mosaic Cropland	Cropland, irrigated or post-flooding
Cropland/Mosaic Cropland	Mosaic cropland (>50%) / natural vegetation (tree, shrub, herbaceous cover) (<50%)
Cropland/Mosaic Cropland	Mosaic natural vegetation (tree, shrub, herbaceous cover) (>50%) / cropland (<50%)
Grassland	Herbaceous cover
Grassland	Grassland
Urban areas	Urban areas
Broadleaf Deciduous Forest	Tree cover, broadleaved, deciduous, closed to open (>15%)
Broadleaf Deciduous Forest	Tree cover, broadleaved, deciduous, closed (>40%) (61)
Broadleaf Deciduous Forest	Tree cover, broadleaved, deciduous, open (15-40%) (62)
Broadleaf Evergreen Forest	Tree cover, broadleaved, evergreen, closed to open (>15%)
Needleleaf Forest	Tree cover, needleleaved, evergreen, closed to open (>15%)
Needleleaf Forest	Tree cover, needleleaved, evergreen, closed (>40%) (71)
Needleleaf Forest	Tree cover, needleleaved, evergreen, open (15-40%) (72)
Needleleaf Forest	Tree cover, needleleaved, deciduous, closed to open (>15%)
Needleleaf Forest	Tree cover, needleleaved, deciduous, closed (>40%) (81)
Needleleaf Forest	Tree cover, needleleaved, deciduous, open (15-40%) (82)
Mixed Forest	Tree cover, mixed leaf type (broadleaved and needleleaved)
Mosaic Forest	Mosaic tree and shrub (>50%) / herbaceous cover (<50%)
Mosaic Forest	Mosaic herbaceous cover (>50%) / tree and shrub (<50%)
Flooded Forest	Tree cover, flooded, fresh or brakish water
Flooded Forest	Tree cover, flooded, saline water
Shrubland	Shrubland
Shrubland	Shrubland evergreen
Shrubland	Shrubland deciduous
Wetland	Shrub or herbaceous cover, flooded, fresh/saline/brackish water
Barren	Lichens and mosses
Barren	Sparse vegetation (tree, shrub, herbaceous cover) (<15%)
Barren	Bare areas
Barren	Consolidated bare areas
Barren	Unconsolidated bare areas

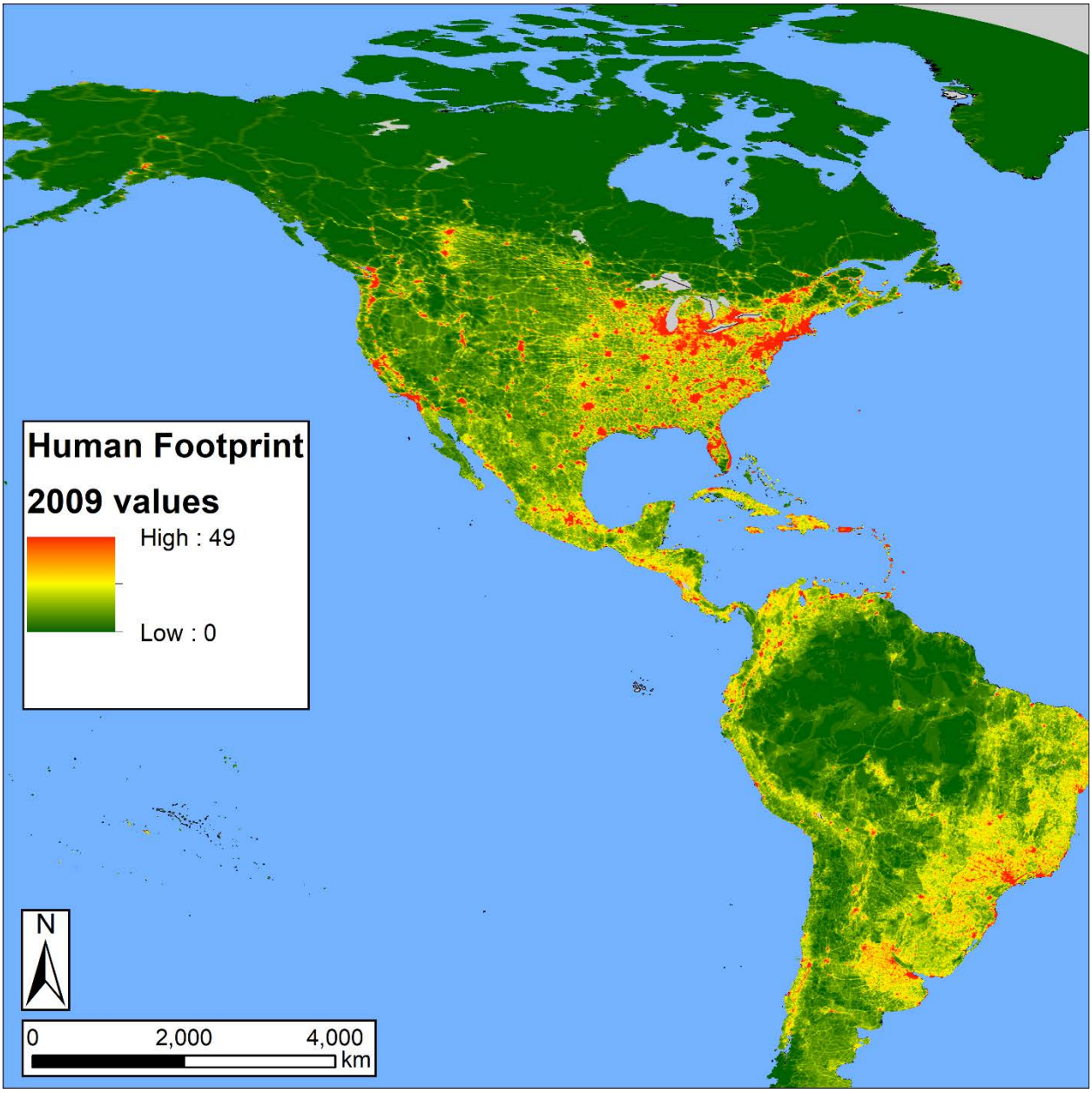



Fig S1. Human footprint estimated in 2009[15].