



Landscape-based population viability models demonstrate importance of strategic conservation planning for birds



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ABSTRACT

Efforts to conserve regional biodiversity in the face of global climate change, habitat loss and fragmentation will depend on approaches that consider population processes at multiple scales. By combining habitat and demographic modeling, landscape-based population viability models effectively relate small-scale habitat and landscape patterns to regional population viability. We demonstrate the power of landscape-based population viability models to inform conservation planning by using these models to evaluate responses of prairie warbler (*Dendroica discolor*) and wood thrush (*Hylocichla mustelina*) populations in the Central Hardwoods Bird Conservation Region to simulated conservation scenarios. We assessed the relative effectiveness of habitat restoration, afforestation, and increased survival and differed placement and levels of effort for implementing those approaches. Population projections of the two species confirmed the potential for large-scale conservation to sustain regional populations. For example, abundances of prairie warblers and wood thrush tripled under afforestation and increased survival scenarios, respectively. Furthermore, responses to conservation actions were driven by interacting local and large-scale population processes such as source–sink interactions and dispersal. Relying on randomly placed habitat conservation was ineffective and potentially counterproductive whereas strategic placements resulted in greater populations and viability of prairie warbler and wood thrush. These models offer a valuable advance in conservation planning because they allow an understanding of the effects of local actions on regional growth, which is necessary for translating regional goals into local actions.

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1. Introduction

The scale of biodiversity loss and threats that cause it require conservation efforts at large scales. Among the major drivers of modern species loss are changes in land use that result in habitat loss, degradation, and fragmentation (Sodhi et al., 2009). These processes and other human impacts operate at scales up to hundreds of square kilometers (Fahrig and Merriam, 1994; Lambeck and Hobbs, 2002). As a result, isolated local-scale efforts to solve a conservation problem are often ineffective (Gutzwiller, 2002). Thus, more focus has been given to planning conservation at large scales (Millsbaugh and Thompson, 2009; Trombulak and Baldwin, 2010). Recognition that successful conservation and natural resources planning must consider more than just site-level management has led to collaboration across agency and ownership boundaries. Examples of this shift in the US include Joint Ventures (e.g. Loesch et al., 1995, www.fws.gov/birdhabitat/jointventures/index.shtm) and more recently Landscape Conservation

Cooperatives (USFWS, 2010), which recruit federal and state agencies and other organizations to plan and implement conservation in ecologically distinct regions with similar communities, habitats, and issues (Fitzgerald et al., 2009).

Conservation cooperatives and joint ventures possess much knowledge and tools to plan and implement conservation, however, they generally lack a framework to integrate these components to consider the predicted effects of a range of conservation actions on populations. Large-scale conservation throughout the world relies heavily on the establishment and management of reserves or protected areas (Chape et al., 2005; Turner and Pressey, 2009). Systematic conservation planning can optimize selection of protected areas that best represents biodiversity (Margules and Pressey, 2000; Possingham et al., 2006) but generally fails to explicitly address long-term viability of individual species of concern (Jonsson and Villard, 2009; Lambeck and Hobbs, 2002; except see Newbold and Siikamäki, 2009). Many governments are increasingly supplementing ownership and management of public resources with market-based or cost-share conservation policies enacted on private lands (Gordon et al., 2011; Rey Benayas et al., 2009). The US invests large amounts of money in privately held

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land through conservation programs (Haufler and Kernohan, 2009), which joint ventures, for example, use to fund on-the-ground application of conservation practices within their respective Bird Conservation Regions (BCR; U.S. North American Bird Conservation Initiative Committee, 2000). Although joint ventures, such as the Central Hardwoods Joint Venture (CHJV), have developed habitat models to inform decisions about conservation, without a means to evaluate the effects of local actions on regional population growth, planners have a limited ability to guide activities (e.g., land or easement purchases, regulation changes, and legislation or land-use planning initiatives) to obtain meaningful impacts on targeted populations (Wells, 2010). A framework is needed which allows planners to be explicit about objectives, strategies, costs, and the population effects of conservation actions.

Landscape-based population viability models can be used to inform large-scale conservation planning because they integrate habitat- and demographic-modeling approaches at a relevant scale, directly relating habitat to population growth (Akçakaya et al., 2004; Bonnot et al., 2011; Larson et al., 2004). Population viability models can be used to evaluate simulated management scenarios (McCarthy et al., 2010) and their spatially-explicit nature lends them to strategic conservation planning. The models consider risk and viability which is fundamental to making sound decisions when assessing and designing alternative management strategies (Millsbaugh et al., 2009). Bonnot et al. (2011) extended landscape-based population viability models for prairie warblers and wood thrush to a regional scale through a combination of habitat, demographic, and dispersal modeling that captured processes ranging across scales, thus providing the ability to link local conservation actions to regional growth and viability.

We demonstrated the utility of landscape-based population viability models to inform large-scale conservation for two migrant songbirds of the Midwestern United States by evaluating conservation scenarios for the Central Hardwoods BCR (CHBCR). We developed representative scenarios to address considerations that plague regional planners such as whether conservation is more effective by managing or restoring current forests to increase habitat quality or to create additional forest to reduce the effects of fragmentation on reproduction. Furthermore, we evaluated the effects of random or opportunistic placement of conservation activities versus strategic management focused on protected areas and population sources. We evaluated multiple levels of effort for each approach to identify what levels are sufficient to reach conservation targets. Finally, we considered how our conservation scenarios, which were inherently ecosystem based (i.e., they focused on a subset of ecosystem processes and structure), impacted 2 species with different life histories.

2. Methods

2.1. Study area

Significant changes to the habitats of the CHBCR have placed bird species at risk in the region (Fig. 1). The CHBCR is approximately 33-million ha in size, covering portions of 10 states in the center of the conterminous United States (U.S. North American Bird Conservation Initiative Committee, 2000). While much of the land that was historically forested remains so today, woodlands and other communities have been dramatically altered (Fitzgerald et al., 2005). Widespread logging in the early part of the 20th century and fire suppression in subsequent decades resulted in conversion of glade, barren, and pine woodland habitats to oak or oak-pine forests. Forests in this region have also been fragmented by agriculture and urban development.

These threats coupled with declines in regional populations has resulted in concern for multiple species, including prairie warblers

(*Dendroica discolor*) and wood thrush (*Hylocichla mustelina*), by Partners in Flight (Panjabi et al., 2005) and the U.S. Fish and Wildlife Service (USFWS, 2002). Prairie warblers are declining by an estimated 2.4% annually (Sauer et al., 2011). Known to breed in shrubby vegetation under an open canopy such as in glades, abandoned fields, and regenerating forests, their decline is likely the result of loss of this habitat over much of the region, combined with reduced productivity due to parasitism associated with fragmentation (Bonnot et al., 2011). Wood thrush are much more abundant than prairie warblers because they are distributed throughout closed canopy, mid-successional forest, which is abundant in the region. However, wood thrush numbers are declining 0.5% annually (Sauer et al., 2011) and declines are at least partly due to higher predation and parasitism in fragmented forests (Robinson et al., 1995).

2.2. Modeling approach

We evaluated population responses of prairie warbler and wood thrush to alternative conservation scenarios using the landscape-based population viability models developed by Bonnot et al. (2011). A detailed overview of these models can be found in Appendix A. The models link populations to landscapes by treating ecological subsections (Bailey et al., 1994) within the CHBCR as subpopulations and basing their demographics on cell-level habitat and landscape attributes. The model determines initial abundance and carrying capacity (K) for a species in each subpopulation using Habitat Suitability Index (HSI) models previously developed specifically for the CHBCR (Tirpak et al., 2009b). These models predict habitat suitability of cells based on their attributes of the cell, including land cover, forest successional stage, canopy cover, and stem density and of the surrounding landscape such as patch size, interspersed and distance to edge (Appendix A). The model also incorporates a Relative Productivity Index (RPI), which is based on the amount of forest cover in a 10-km radius and edge within a 200-m radius (Appendix A). It represents the prevailing theory that productivity of Midwestern songbirds declines in response to increasing brood parasitism and nest predation as forest cover in the landscape decreases and local edge density increases (Lloyd et al., 2005; Robinson et al., 1995; Stephens et al., 2004; Thompson et al., 2002). Demographic information is combined into stage-based matrices which contain survival and fertility rates identified in the literature (although fertility is adjusted for relative productivity). Growth is projected stochastically and under density dependence in RAMAS Metapop 4.0 (Akçakaya, 2002). The model also incorporates annual dispersal by combining the proportion of each subpopulation that dispersed with estimates of the cell-based movements of those dispersers to the surrounding populations based on distance and the quality of their habitat.

The accuracy of the landscape-based viability models and their components has been verified against current regional data. The performance of the HSI models in identifying habitat suitability was verified and validated with regional abundance data from the North American Breeding Bird Survey (BBS; Tirpak et al., 2009a). While the RPI has not been validated it has a strong conceptual basis based on the original studies reporting these effects (Donovan et al., 1997; Robinson et al., 1995; Thompson et al., 2002) and subsequent reviews and meta-analyses (Chalfoun et al., 2002; Lloyd et al., 2005; Stephens et al., 2004). Ultimately, Bonnot et al. (2011) verified their population trends projected for the current landscape within 2.0% (now 1.8%) of the BBS's empirically observed regional trends, noting that the estimates might have been closer except that BBS trends reflected changes to the landscape, specifically the decline and fragmentation of habitat, over a period leading up to 2001, whereas their model was based only on the current landscape in 2001.

We constructed scenarios for habitat restoration, afforestation, and reduced mortality and considered both random and strategic placement of restoration and afforestation activities. These scenarios reflected contrasting ecosystem-based approaches because they addressed different ecosystem components and processes since altered in the region. For example, restoration restored existing forest to appropriate natural communities while afforestation converted non-forested crop and pasture land to forest. The nature of these changes as they are used by the HSI and RPI models above implied that restoration would primarily affect carrying capacity because it improved suitability of currently existing forested habitat and afforestation would affect carrying capacity and productivity because it added forested habitat and reduced fragmentation. Efforts to reduce mortality would increase survival in these birds. Although none of these approaches targeted prairie warblers or wood thrush specifically, differences in their habitats, life histories and population sizes might suggest different responses among these scenarios. We simulated population responses to habitat restoration and afforestation scenarios by changing habitat attributes of patches in the landscape and then simulating population change with our population model. We simulated population responses to reduced mortality by directly changing annual survival rates in the population model. Although we realize that rates at which conservation can actually be implemented differs among the approaches, our scenarios were not dynamic but represented the desired future conditions or fully implemented conservation plans sustained for the duration of the population simulation.

2.3. Habitat restoration

We simulated habitat restoration that would restore current forests to their potential natural forest communities (i.e., savanna, woodlands, and forest) and thus affect carrying capacity (K) for prairie warbler and wood thrush (Table 1). Restoration was based on habitat targets developed by the CHJV to meet their and Partners in Flight's population goals for breeding birds in the region

(Jones-Farrand et al., 2009; Rich et al., 2004). The targets are ecosystem-based and focus on management such as prescribed burns and timber harvests to restore natural forest communities specified by an ecological potential model (L.E. O'Brien, D.T. Jones-Farrand and J.A. Fitzgerald, unpublished data). The ecological potential model characterizes 11 forested or semi-forested native communities in the CHBCR according to land-type associations, landform positions, and assumed historic disturbance regimes (Appendix B). We considered any currently forested cell that had the potential for one of the selected natural communities as a candidate for restoration (Table 1). We identified current forest classes from the 2001 National Land Cover Dataset (NLCD; Homer et al., 2004). We used the ecological potential model to identify the target for restoration for each cell. We assumed public and private landowners would treat patches rather than individual cells so we grouped candidate cells into contiguous patches and dissected the patches by roads to more realistically simulate management at an ownership scale. Lastly, we considered only candidate patches ≥ 4.05 ha (10 ac) as a practical measure from a public land manager's perspective as well as to reflect the restrictions used by private lands programs (L. Heggemann, personal communication).

We implemented random placement of restoration by randomly selecting candidate patches from all ownerships to reflect the potential opportunistic nature of private lands management (Fig. 2). We simulated strategic placement of restoration by selecting candidate patches with levels I–VI protection in the protected areas database for the US (USGS, 2011). When restoration efforts exhausted all available protected land we continued on adjacent patches, weighted by distance to protected area. We selected patches until objectives for the individual natural communities were filled, which totaled approximately 2,000,000 ha, and also considered the impacts of only meeting 50% of these goals and restored 1,000,000 ha (Table 1). The CHJV partners actually restored approximately 50,000 ha of forest communities in 2011 (D.T. Jones-Farrand, unpublished data), thus while our targets were ambitious we believe they are relevant. Although selection

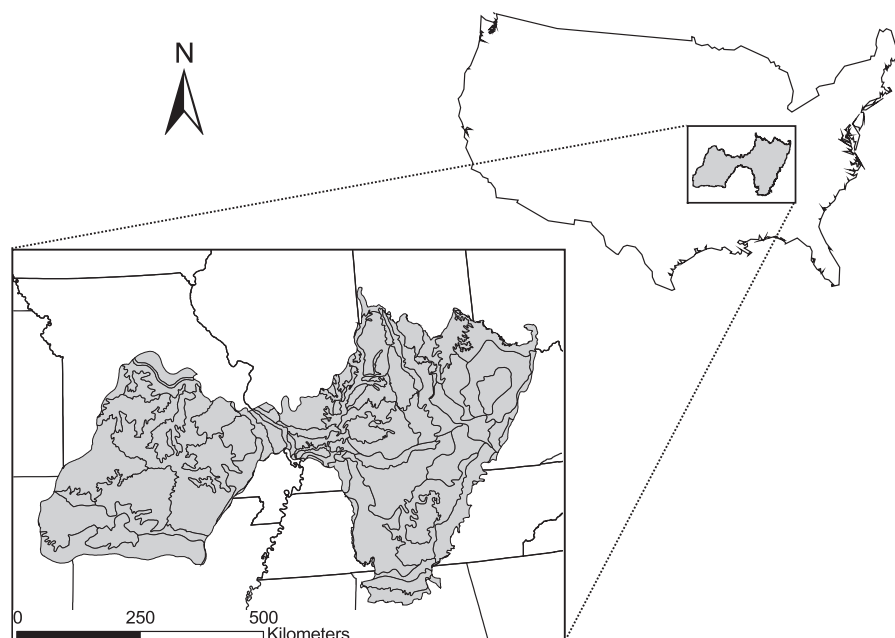


Fig. 1. A map of ecological subsections within the Central Hardwoods Bird Conservation Region, located in the central U.S. Subsections were treated as subpopulations in an ecoregional, landscape-based population model.

Table 1

Descriptions of conservation scenarios simulated across the Central Hardwoods Bird Conservation Region evaluated using landscape-based population viability models for prairie warblers and wood thrush.

Approach	Objective	Current landcover ^a	Potential community ^b	Placement	Effort
Habitat restoration	Increase carrying capacity in subpopulations through restoration of existing forest patches to their potential states to improve suitability	Deciduous, mixed, and evergreen forests; scrub-shrub; woody wetlands	Prairie/savanna; savanna/barrens; glade/woodland mosaic; oak open woodland; oak closed woodland; pine/bluestem open woodland; pine/oak closed woodland; upland mesic forest; floodplain forest	Strategic: candidate patches ≥ 4.05 ha (10 ac) on protected areas first, then on private land, weighted by distance to protected area	2,000,000 ha ^c 1,000,000 ha ^c
				Random: candidate patches ≥ 4.05 ha (10 ac) at random throughout the region	2,000,000 ha 1,000,000 ha
Afforestation	Increase reproductive productivity of subpopulations through conversion of currently non-forested land to forest to increase forest cover and reduce fragmentation	Grassland/herbaceous; pasture/hay; cultivated crops; herbaceous wetlands	Glade/woodland mosaic; oak open woodland; oak closed woodland; pine/bluestem open woodland; pine/oak closed woodland; mesic forest; floodplain forest	Strategic: candidate patches of any size, weighted by the percent of forest cover within 10 km	2,000,000 ha; 1,000,000 ha 300,000 ha
				Random: candidate patches of any size at random throughout the region	2,000,000 ha 1,000,000 ha 300,000 ha
Survival	Increase survival in juvenile and adult stages through actions that reduce anthropogenic mortality from communication towers			All individuals throughout the region	5% 1%

^a Landcover types in the 2001 NLCD that were candidates for conservation action under the given approach.

^b Potential natural forest community considered amenable to the given approach. Cells having the potential to be one of the listed communities were considered candidates for undergoing conservation action.

^c Amounts of land treated under habitat restoration scenarios were based on all (2,000,000 ha) and half of the habitat objectives planned by the Central Hardwoods Joint Venture, the coordinating body for bird conservation in the region.

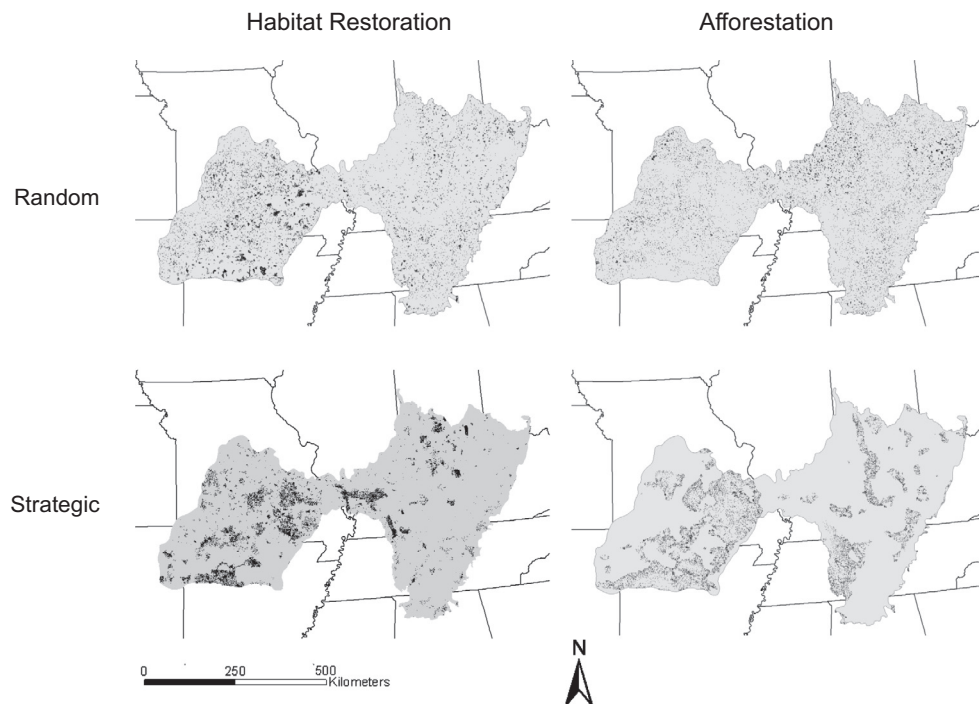


Fig. 2. Placement of 2,000,000 ha of habitat conservation in the Central Hardwoods Bird Conservation Region. Black areas indicate patches selected at random or strategically on protected areas for habitat restoration. Under the afforestation scenario, patches were selected at random or strategically based on the proportion of the surrounding landscape that was forested.

occurred at the patch level, restoration individually affected cells based on their potential natural community and we only restored cells with natural communities with unmet objectives.

Once selected, we converted forest patches to their respective natural communities by changing the landcover and structural attributes of their cells to agree with the characteristics of the nat-

ural communities (Table 2). We focused on the attributes used by the HSI models and assigned restored cells to a forest successional stage and landcover and values of canopy cover and small stem densities that were appropriate for each natural community, assuming that agencies would restore and maintain them through active management (Table 2). Given that much of the forest in this

Table 2

Potential natural communities used to guide habitat restoration simulations. Patches of forest were selected until acreage objectives for the natural communities were individually fulfilled for the given scenario. Under the habitat restoration scenarios, the landcover, seral age, canopy cover, and small-stem density of restored patches were characterized on the basis of the potential natural community. Acreage objectives were derived from Partners in Flight population goals according to Jones-Farrand et al. (2009).

Potential natural community ^a	Acreage objectives (ha)	Landcover ^b	Seral age ^c	Canopy cover ^d	Small-stem density ^e
Prairie/savanna	11,644	Deciduous	Shrub-seedling – sapling	10	6000
Savanna/barrens	26,064	Deciduous	Shrub-seedling – sapling	10	6000
Glade/woodland mosaic	76,959	Deciduous	Shrub-seedling	5	8000
Oak open woodland	539,209	Deciduous	Shrub-seedling – saw	40	10,000
Oak closed woodland	298,027	Deciduous	Pole – saw	70	4000
Pine/bluestem open woodland	62,647	Evergreen	Shrub-seedling – saw	40	6000
Pine/oak closed woodland	62,309	Mixed	Pole – saw	70	4000
Mesic forest	691,486	Deciduous	Pole – saw	90	2000
Floodplain forest	197,678	Woody wetlands	Pole – saw	90	2000

^a Potential natural communities are outlined by L.E. O'Brien, D.T. Jones-Farrand and J.A. Fitzgerald (unpublished data).

^b National landcover data classification.

^c Patches were randomly assigned to one of a range of seral ages appropriate for the potential natural community.

^d Percentage of canopy cover specified for cells in restored patches.

^e Densities of small stems (stems/ha) specified for cells in restored patches.

region was closed-canopy mature forest, many of the changes converted forest to glades, savanna, and woodland communities. However, closed forest remained a major component of the landscape.

2.4. Afforestation

Farmland abandonment and afforestation worldwide effectively restore ecosystem function that recovers biodiversity (Chazdon, 2008). Our afforestation scenarios reflected this process by simulating conversion of non-forest lands to forest, potentially reducing fragmentation. We used the NLCD and ecological potential model to identify cells in the region that were currently grassland or agriculture but had the potential to be one of the forested communities, including glades, savannas, woodlands, and forests (Table 1). We grouped contiguous cells into candidate patches to reflect the scale of land conversion processes such as conservation easements or farmland abandonment. For strategic afforestation, we weighted patch selection by the percent of forest cover within 10 km to focus efforts in areas of the region that have the greatest bird productivity (Bonnot et al., 2011; Robinson et al., 1995). We simulated afforestation of 2,000,000 ha and 1,000,000 ha, to compare with restoration scenarios and also 300,000 ha (1% of the region) because we thought afforestation might occur on less area because of greater costs or slower implementation.

For the selected patches, we specified the landcover of cells according to their potential natural communities (Table 3). However, we assumed afforested patches would not be actively managed following their initial creation and characterized the structural attributes of their cells to reflect the existing conditions of the region's forest as indicated by Forest Inventory and Analysis (FIA) data (Table 4). For example, we randomly assigned patches forest ages from a distribution that reflected current forest ages and based canopy closure and stem density values on their relationships with forest ages from regional FIA data. Thus, afforestation added forests to the region, but the habitat resembled what is currently there.

2.5. Survival

We considered the effects of increasing survival to address a potential conservation measure not focused on breeding habitat. For example, the impact of communication towers on migrating birds has recently received increased attention and offers an approach to reducing mortality of birds across large-scales through lighting and structural changes (Gehring et al., 2009; Longcore et al., 2012). However, in the absence of data on species-specific mortality impacts from these changes, we evaluated scenarios with a 1% and 5% increase in adult and juvenile survival while maintaining the

Table 3

Cells within forest patches created under afforestation scenarios were characterized for landcover on the basis of the potential natural community indicated by the ecological potential model.

Potential natural community ^a	Landcover ^b
Glade/woodland mosaic	Deciduous
Oak open woodland	Deciduous
Oak closed woodland	Deciduous
Pine/bluestem open woodland	Evergreen
Pine/oak closed woodland	Mixed
Mesic forest	Deciduous
Floodplain forest	Woody wetlands

^a Potential natural communities are outlined by L.E. O'Brien, D.T. Jones-Farrand and J.A. Fitzgerald, (unpublished data).

^b National landcover data classification.

current landscape. Although we are uncertain of the feasibility of achieving these targets, 1% and 5% increases represented reducing mortality of the prairie warbler population's initial 134,628 adult females by 838 and 4188, respectively. We thought these scenarios were reasonable, given that the total annual prairie warbler mortality due to towers in North America is estimated >30,000 birds (>2% of their population; Longcore et al., 2013).

2.6. Model application

We applied the wood thrush and prairie warbler models to the simulated landscapes to estimate each population's demographic parameters based on HSI and RPI values summarized across sub-sections (Bonnot et al., 2011). We recalculated HSI and RPI values and estimated demographic parameters according to Bonnot et al. (2011), with two exceptions (Appendix A). To provide a more realistic and conservative estimate of regional K, we required individual habitat patches to support at least 1 territory to be included in K for each subpopulation. As a reference, we recalculated K from the original models based on the current landscape. Secondly, we based initial abundance for all simulations on the current landscape scenario and ran 1000 stochastic simulations over 100 years for each scenario in RAMAS GIS 4.0 (Akçakaya, 2002). We evaluated impacts of conservation scenarios on growth and viability for each species using the population's projected abundance over 100 years and the probability of declining from the initial population size by more than 25%.

3. Results

Revised estimates of K and initial abundance for the current scenario resulted in lower projected abundances than Bonnot

Table 4

The structure of cells within forest patches created under afforestation scenarios were characterized according to the seral age assumed for the patch. Newly created forest patches were randomly assigned ages from a distribution that reflected both current forest ages and the addition of new forest (e.g., 10% of new forest patches were assumed to be of grass/forb and shrub/seedling ages, each).

Seral age	Percent of patches ^a (%)	Canopy cover ^b (%)	Small-stem density ^c
Grass-forb	10	0	250
Shrub-seedling	10	5	3500
Sapling	20	20	1000
Pole	30	55	8000
Saw	30	70	6500

^a Percentage of new forest patches characterized with the given seral age.

^b Percentages of canopy cover for cells in afforestation patches reflect the average canopy cover for each seral age in the current landscape (T. Bonnot, unpublished data).

et al. (2011) but had little effect on projected growth trends. Under current conditions prairie warblers declined 0.50% annually, from an initial 134,628 breeding females. Wood thrush declined 0.05% annually from an initial population of 348,724 breeding females (Fig. 3).

Overall, habitat restoration and afforestation increased prairie warbler and wood thrush habitat. Restoring 1,000,000 and 2,000,000 million ha of the region's forest to the different natural communities more than doubled (>300,000 extra birds) and tripled (>600,000 birds) prairie warbler K, respectively. Wood thrush experienced smaller increases in K from habitat restoration; the changes in all scenarios supported 75,884–257,290 extra individuals (<10% increase in K). Afforestation, however, produced similar increases in wood thrush and prairie warbler K, ranging from 40,000 to 300,000 additional birds depending on the amount of forest created. But these increases were much more substantial for prairie warblers given their originally low carrying capacity. Ultimately, the relative impacts of increases in K, as well as afforestation's effects on productivity and the increases survival can only be assessed by examining the resulting population growth.

Prairie warbler growth benefited from all three approaches but not all placements. Random restoration and afforestation scenarios did not reverse prairie warbler declines, while strategic restoration and afforestation scenarios resulted in increasing populations (Fig. 3). Randomly converting 300,000 ha of land to forest promoted greater declines than current conditions. Prairie warbler population growth improved most through strategic afforestation that converted 2 million ha of non-forest to forest, and exceeded 400,000 breeding females in 100 years due to 1% annual growth (Figs. 3 and 4). There was less of a response to strategic afforestation when fewer hectares were converted and when afforested randomly. Strategically restoring 1,000,000 ha of natural communities, including glades, in protected areas allowed 60% more growth in prairie warblers than restoring randomly selected patches. However, the added effort to restore 2,000,000 ha versus 1,000,000 ha resulted in only marginal increases in growth and viability (Figs. 4 and 5). In general, strategic habitat restoration and afforestation produced similar abundances in prairie warblers, but the population was twice as viable when simulating afforestation (Fig. 5). Increasing survival clearly improved the viability of the prairie warbler population even though increases in abundance were not as substantial as habitat-based approaches. Although abundances resulting from a 5% increase in survival were not as large as when restoring or creating habitat, the population had virtually no chance of declining $\geq 25\%$ (Figs. 4 and 5).

Habitat restoration had slightly positive effects on regional wood thrush growth given the prevalence of their habitat in the region. The ecosystem-based focus on converting closed forest to open natural communities reduced wood thrush capacities locally in areas, but much of their habitat, remained intact. Rather, compared to restoration, increases in survival and the increase in productivity from intensive afforestation more than quadrupled and

doubled the population's abundance, respectively (Fig. 4). The greatest growth was obtained by increasing survival 5%, which resulted in a 6-fold increase in abundance from the start of the simulation. Both habitat-based approaches still improved the population's viability. For example, strategically restoring 1,000,000 ha of forest increased abundance in 100 years by 13%, and reduced the probability of a 25% decline during that time by 18 points over the current scenario (Fig. 5.). Both the level of effort and placement of afforestation affected wood thrush.

4. Discussion

Our use of population modeling revealed the potential complexity of bird population responses to conservation scenarios. The effectiveness of conservation scenarios depended on the approach, placement, effort, and species. As expected, wood thrush and prairie warblers responded to habitat restoration differently given their different life histories. However, other patterns resulted from more complex interactions among demographic processes such as density dependence, local abundance, productivity, and dispersal. For example, differences among strategic and random scenarios were in part due to source-sink dynamics, which are the result of an interaction between dispersal and landscape effects on productivity. It was these interactions that allowed Bonnot et al. (2011) to capture processes such as area sensitivity and source-sink dynamics that were critical to initially tracking regional growth. And it is these interactions that appeared to drive regional population responses to conservation scenarios. Therefore, because the effectiveness of scenarios at sustaining species ultimately depends on interacting factors such as life history, occupancy patterns, population size, K, dispersal, and productivity; a number of considerations important for regional conservation planning were demonstrated in our results.

4.1. Habitat-based conservation is most effective when it's implemented strategically

Comparisons between the placements of habitat conservation demonstrated the importance of regional scale, source-sink dynamics for deciding where to invest conservation resources. Randomly placed afforestation failed to increase bird productivity enough in most sink landscapes to have the desired outcome of converting subpopulations to sources (Fig. 6). Rather, strategically adding forest in heavily forested landscapes improved bird productivity in existing source populations and created additional sources from nearby sinks, thus supporting a conservation strategy of maximizing the ratio of source to sink habitat to sustain bird populations (Robinson and Hoover, 2011). If sink landscapes are targeted, however, sufficient forests must be created to overcome sink thresholds and achieve beneficial results. Otherwise, if forest cover is added at levels insufficient to improve productivity

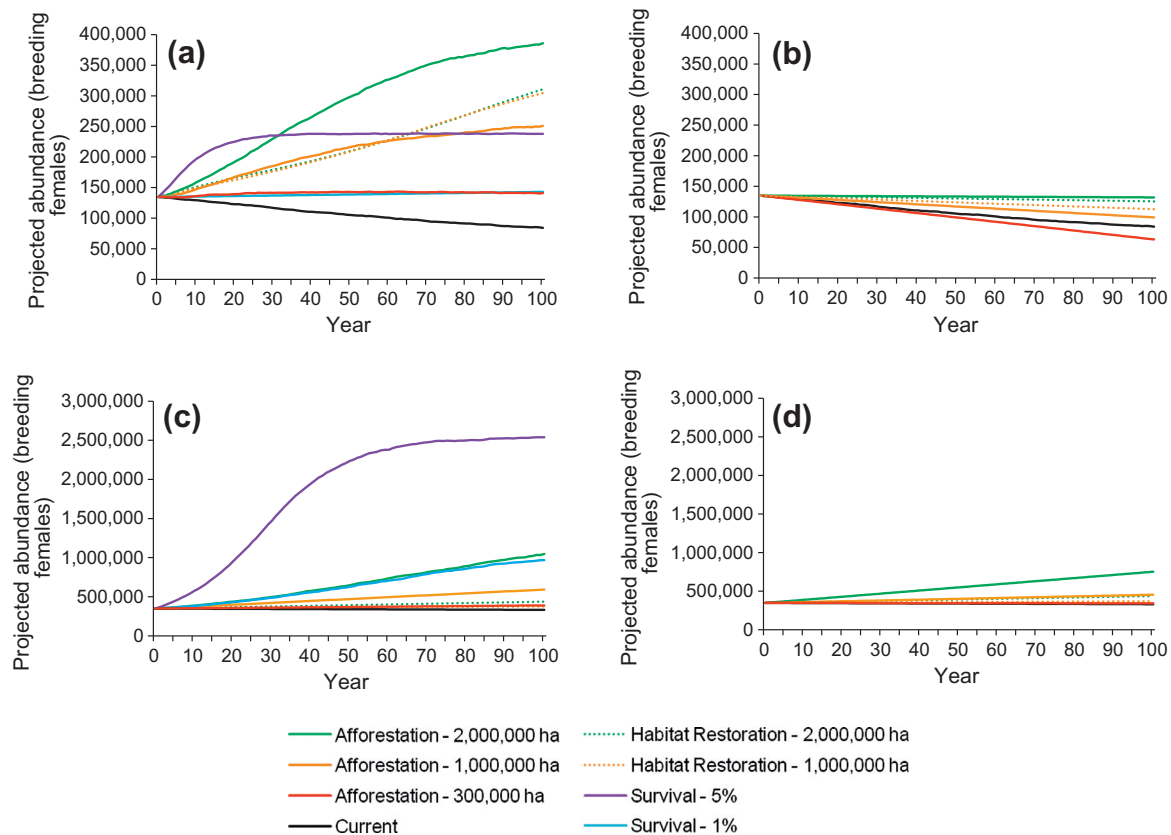


Fig. 3. Projected population responses by breeding birds over 100 years in response to simulated conservation scenarios. Prairie warblers benefited from increases in survival and strategically placed habitat conservation (a), however, randomly placed conservation (b) failed to reverse the prairie warbler's declines. Wood thrush also responded more to increases in survival and strategically placed habitat conservation (c) than to random efforts (d). The current scenario assumes the current landscape with no changes.

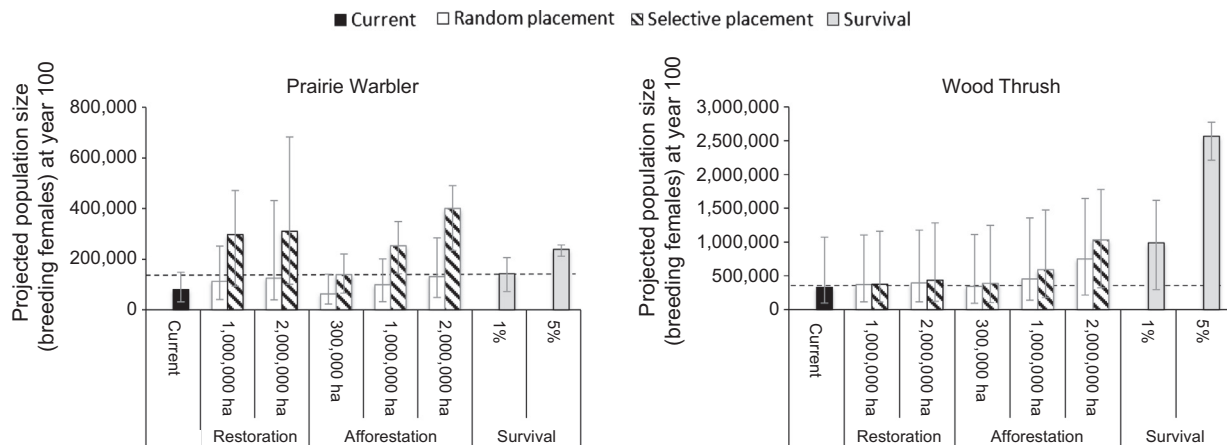


Fig. 4. Projected response of regional prairie warbler and wood thrush population sizes to simulated conservation scenarios. Strategic habitat restoration targeted habitat on protective areas, while strategic afforestation created forests in highly forested, productive landscapes. The current scenario assumes the current landscape with no changes. Bars convey the median projected population size of breeding females at the end of the simulation and are bounded by the 5th and 95th percentiles. The horizontal dashed line indicates the initial population size.

enough to obtain positive growth, the population will still act as a sink. While these thresholds are currently difficult to identify, this knowledge could prove important to future planning. For now, the difference between random and strategic placements should warn programs against basing incentives only on the quality of habitat patches without consideration of the surrounding landscape; land managers could be using valuable resources to implement land management practices that are considered conservation-friendly

but provide little benefit because the overall landscape is unsuitable for growth (i.e., is a sink) (Gimona et al., 2011).

Similarly, both populations responded more to habitat restoration when those actions strategically occurred on protected lands. The prairie warbler population was half as likely to decline under strategic than random restoration. This result was surprising given that restoration, unlike afforestation, did not directly target source populations and prairie warblers were potentially limited by low

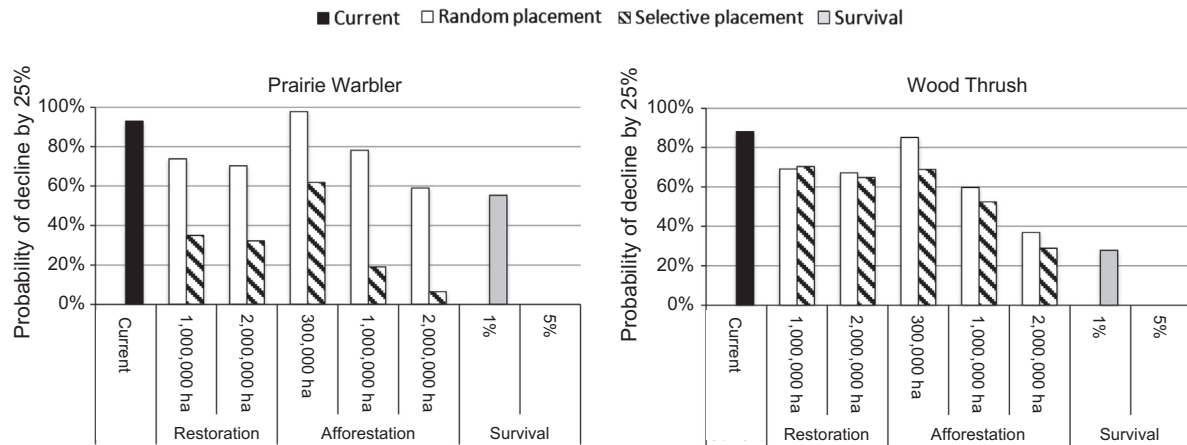


Fig. 5. Projected viability of prairie warbler and wood thrush populations resulting from conservation scenarios. Strategic habitat restoration targeted habitat on protected areas, while strategic afforestation created forests in highly forested, productive landscapes. Bars indicate the probability of the regional population declining by 25%. The current scenario assumes the current landscape with no changes.

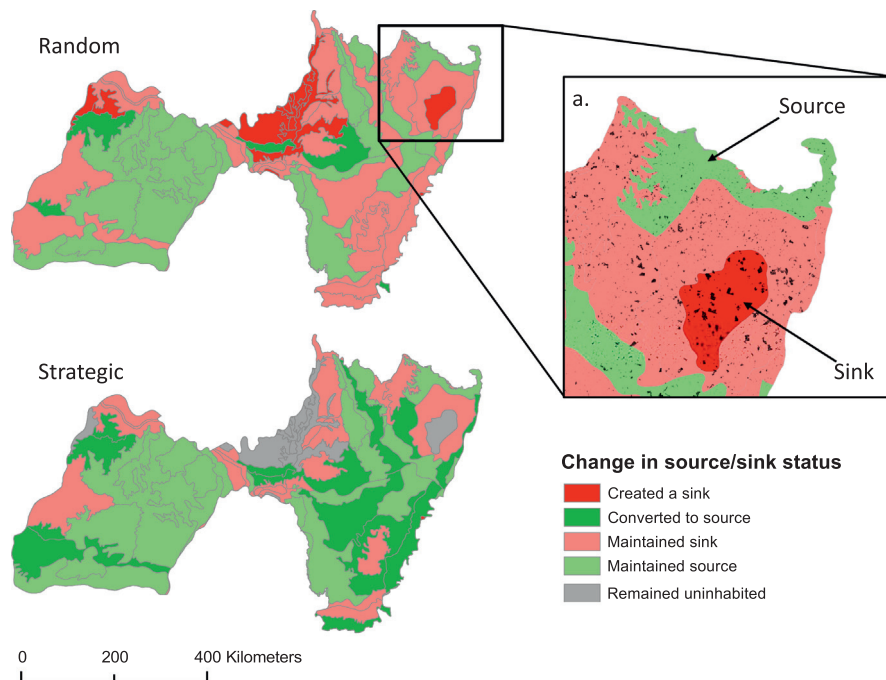


Fig. 6. Contrasting impacts of random and strategic placements of 1,000,000 ha of afforestation on the growth of prairie warbler subpopulations across the Central Hardwoods Bird Conservation Region. The creation of new forests in the region were intended to reduce fragmentation, thus increasing productivity and promoting growth, especially in what are currently estimated to be sink landscapes. However, randomly placed afforestation failed to create forests at levels that would convert sink populations into sources. Whereas strategically placed afforestation converted numerous sink populations into sources, random efforts actually created sinks with the potential to act as ecological traps. For example, as a result of the random afforestation, shown as black patches in the insert (a), the carrying capacity of the Inner Bluegrass subpopulation (sink) increased from 0 to 5209 adult females, causing 7% of the dispersers from a nearby source to then immigrate into the sink which declined annually at 8.3%.

productivity (Bonnot et al., 2011). However, restoration on protected areas actually increased K in productive landscapes because many protected areas in this region are state and national forests, which are clustered in heavily forested landscapes. The increased productivity by birds that dispersed to these areas contributed to regional growth. Even wood thrush, whose overall K and projected abundance changed little from restoration scenarios, saw an increase in viability as their distribution shifted and a greater proportion of breeding occurred in productive landscapes. This interaction between K , productivity, and dispersal reveals that even if a population is not primarily limited by habitat, it can still benefit from habitat restoration, if placed in source landscapes.

4.2. Conservation that impacts multiple demographics could lead to unintended consequences

Our projection that 300,000 ha of random afforestation resulted in greater prairie warbler declines seems counterintuitive – how could more forests hurt growth? This result occurred because afforestation affected dispersal and breeding differently. Random afforestation of 300,000 ha failed to sufficiently alter landscapes of most subpopulations to increase productivity but it added habitat in what remained sink populations, consequently drawing more dispersers to breed at lower productivities in situations resembling ecological traps (Fig. 6; Donovan and Thompson,

2001). These changes affected dispersal and breeding productivity differently because they are based on different processes at different scales. Dispersal movements were partly determined by a patch's local habitat attributes in the HSI, whereas productivity was based on characteristics of the larger landscape captured by the RPI (see Appendix A). The likelihood that this pattern resembling ecological traps constitutes a real consequence is supported empirically by cases where selection of a habitat no longer agrees with the ultimate fitness benefits of that habitat (Battin, 2004; Robinson and Hoover, 2011; Robertson and Hutto, 2006). Indeed, forest fragmentation is a relatively new anthropogenic disturbance and forest songbirds generally lack adaptations to avoid cowbird parasitism associated with fragmentation (Hoover, 2003). Much of the discussion surrounding ecological traps is rarely incorporated into conservation planning or reserve design approaches. However, these results support other's warnings about the potential impacts of this phenomenon on conservation efforts (Battin, 2004; Donovan and Thompson, 2001). Therefore, it will be important to reduce the risks of ecological traps by considering the landscapes surrounding targeted patches.

4.3. Success of isolated conservation approaches could be limited for populations under multiple stresses

Our habitat-based and survival scenarios represent habitat and natural process restoration (category 2.3) and species recovery (category 3.2) conservation actions that can be applied to address threats facing species as outlined by the International Union for Conservation of Nature, (Salafsky et al., 2008). However, the prairie warbler results illustrate how isolated scenarios that simulated restoration to counteract the threat of regional habitat loss or simulated increased survival from reduced mortality threats were ultimately limited in their effectiveness in the presence of the other threat. The effort to increase K had limited outcomes unless accompanied by increases in productivity or survival that promoted growth. Conversely, the dramatic impacts on growth initially seen by increasing survival 5% eventually dissipated under the pressures of insufficient habitat (Fig. 3). Therefore, successful conservation planning will need to consider all threats limiting regional populations, which can be exceedingly complex for migratory species (Johnson et al., 2009).

4.4. Population metrics and response times

Prairie warbler regional viability was greatest when increasing survival 5% (Fig. 4), even though projected abundance fell short of strategic habitat-based scenarios (Fig. 4). Also, although wood thrush abundance did not respond to habitat restoration, those efforts reduced the probability of declining 25% from its initial size by as much as 20 points (Fig. 5). The changes in habitat concentrated wood thrush in heavily forested landscapes that provided higher productivity and ultimately increased viability. Therefore, it is important to be explicit about metrics and targets when planning (e.g., Millspaugh et al., 2009).

Differences in the response times among approaches stemmed from the demographics they affected. Wood thrush and prairie warbler populations responded quicker and with greater certainty (indicated by the error depicted in Fig. 4) to increases in survival than habitat conservation scenarios and afforestation produced more rapid growth than restoration. These differences occurred because increased survival immediately provided more breeders, afforestation increased the productivity of breeders, and restoration relied on dispersal and subsequent production to enhance growth. Although we modeled desired future conditions and did not address the rates at which conservation can actually be implemented, population projections such as ours provide a basis

for measuring progress in conservation, which is lacking in many bird-focused, ecoregional plans (Wells, 2010). For example, it may take 10–30 years after full implementation to see a measurable response.

4.5. Ecosystem-based approaches could be effective at managing for multiple species

Conservation planning has increasingly turned to ecosystem-based approaches to manage for multiple species in a landscape or region (Drapeau et al., 2009; Redford et al., 2003). Rather than planning for a species' individual habitat requirements, these approaches focus on restoring or maintaining the composition and processes of ecosystems that affect all species (Lambeck, 1997; Lambeck and Hobbs, 2002). The scenarios evaluated here reflect that focus by restoring natural communities that provide a range of habitats and creating forests to reduce fragmentation impacts. Whereas the effectiveness of any scenario in conserving a particular species depends on its ecology, both populations generally responded favorably to all three approaches. Even habitat restoration, which actually removed wood thrush habitat locally in many areas by restoring closed canopy, mature forests to more open or early successional communities, benefited the regional population. However, we provide only two examples of birds. More comprehensive assessments across various species, communities, and taxa are needed to ultimately confirm the effectiveness of ecosystem-based approaches in sustaining biodiversity. At such time, population models, such as those used here, will allow linking species viability targets with ecosystem targets that actually correspond to the tactical and operational tools used by forest managers to achieve conservation goals (Jonsson and Villard, 2009).

5. Conclusions

We demonstrated the potential for large-scale conservation to successfully restore and sustain regional bird populations. The possibility that restoring natural communities in protected areas will conserve multiple bird species is an important development in the ongoing debate about the role of protected areas for sustaining biodiversity (Gordon et al., 2011; McDonald and Boucher, 2011; Mora and Sale, 2011; Possingham et al., 2006). However, these simulations did not address the likelihood of the landscapes surrounding these areas to become increasingly developed and decreasingly functional which would definitely impact growth projections (Davis and Hansen, 2011). Furthermore, budgetary constraints could easily preclude full implementation of protected area restoration. Thus, the prospect that habitat restoration and afforestation on private lands may contribute to regional biodiversity is significant and could empower such programs to efficiently promote local conservation, especially if targeted to productive landscapes. Finally, while we are only beginning to understand the impacts of tower collisions on mortality over a large scale (Longcore et al., 2013), the prospect that structural changes to towers could reduce mortality (Gehring et al., 2009) provides a powerful approach to promoting viability in these birds.

We believe conservation will be more successful when it is strategic, multifaceted, and informed. For example, we have shown that efforts that conserve insufficient habitat in fragmented landscapes will likely fail to achieve desired population responses and could potentially be of greater detriment. Moreover, conservation that is multifaceted with respect to different approaches could overcome the limitations of each approach while capitalizing on strengths. Although the principles we outlined for managers may seem obvious and have been discussed elsewhere, they still are not widely employed, likely because they are not as intuitive as

they seem. For example, what exactly does it mean to be strategic when selecting forests to restore? Without more specific knowledge of what processes are affecting populations, managers lack the basis for implementing specific actions. Landscape-based population models, illustrated in this paper, could improve conservation decisions.

Planners face a paradox whereby translating regional goals into local actions requires understanding the effects of local actions on regional growth. Indeed, responses of regional populations to conservation actions can be complex due to population processes interacting across scales. Thus, when planning conservation at large scales these models could prove valuable to maximizing effectiveness and avoiding unforeseen pitfalls. Currently, they do not incorporate a dynamic landscape, which is necessary given expected climate change impacts and land use changes across the region. Nor do they address the spatially explicit costs of different conservation actions or are currently amenable to optimization methods which would allow identification of best conservation scenarios. Incorporating these components will prove critical to ultimately providing the best guidance for regional conservation.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.biocon.2013.05.010>.

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