



Assessing source-sink stability in the context of management and land-use change

Julie A. Heinrichs · Joshua J. Lawler · Nathan H. Schumaker ·
Lauren E. Walker · David A. Cimprich · Amy Bleisch

Received: 15 June 2018 / Accepted: 24 December 2018 / Published online: 16 February 2019
© Springer Nature B.V. 2019

Abstract

Context Management actions and land-use change can disrupt interdependent population processes, re-define population networks, and change source-sink dynamics. Yet we know little about the types of changes that can de-stabilize source-sink dynamics and how such changes could affect management decisions.

Objectives We examined the degree to which source-sink status and strength could change under a range of management actions and land-use change scenarios including different patterns and extents of

habitat loss, restoration, demographic improvements from parasitism control, and increased frequencies inter-population movement.

Methods We developed an empirically-rich, spatially explicit, individual-based model for the formerly endangered Black-capped vireo in Texas. We simulated the network-wide consequences of different kinds of changes and compared the resulting source-sink strength, status, and regional abundance across scenarios. We gauged source-sink stability by the degree to which system changes caused the reversal of source or sink status.

Results The stability of source-sink characterizations differed with the type of change. Source-sink dynamics were less responsive to small changes to population structure and changes that minimally affected demographic conditions. Source-sink status was most responsive to changes that affected habitat patterns and quality.

Conclusions Accurately classifying sources and sinks is challenging, particularly in variable and directionally changing systems. The stability of source-sink classifications depends on the type of management or land-use change. Management actions may need to weigh interventions that improve regional abundance against those that alter regional source-sink dynamics as abundance and source-sink states can be sensitive to different kinds of change.

Electronic supplementary material The online version of this article (<https://doi.org/10.1007/s10980-018-00768-6>) contains supplementary material, which is available to authorized users.

J. A. Heinrichs · J. J. Lawler · L. E. Walker · A. Bleisch
School of Environmental and Forest Sciences, University
of Washington, P.O. Box 352100, Seattle,
WA 98195-2100, USA

J. A. Heinrichs (✉)
Natural Resource Ecology Laboratory, Colorado State
University, Fort Collins, CO 80523, USA
e-mail: Julie.Heinrichs@colostate.edu

N. H. Schumaker
Department of Fisheries and Wildlife, Oregon State
University, Corvallis, OR, USA

D. A. Cimprich
Natural and Cultural Resources Management Branch,
Environmental Division, Fort Hood, TX 76544, USA

Keywords Black-capped vireo · Source-sink
dynamics · Management · Habitat restoration ·

Spatially explicit individual-based model · Land-use change

Introduction

Forecasting the impacts of management and land-use change is an important part of ecological planning, particularly for species at risk of decline or extinction in non-stationary environments. Predicting the potential responses of wildlife to altered future conditions can indicate the most important changes to track and the most influential factors to weigh in decisions (Hannah et al. 2002; Copeland et al. 2009; Bancroft et al. 2016). In spatially structured populations, the challenge extends beyond assessing changes in habitat and assessing the fates of local populations. In these populations, directional change can affect interdependencies among populations and re-define the resulting population network. In source-sink populations, changes in one population (e.g., destruction of an important source) can alter local conditions, regional flows of individuals, and network-wide persistence. As source-sink populations are connected by migrants moving among sources (net exporters of individuals) and sinks (net importers; Holt 1985; Pulliam 1988), system changes that alter local demographic conditions, carrying capacities, or exchanges of individuals are expected to have multi-scale and network-wide impacts.

Greater conservation benefits are expected if conservation actions are guided by assessments that consider both demography and movement (i.e., source-sink dynamics) rather than simplified population conditions or habitat states that may fail to identify the most important populations. Sources are often presumed to contribute more to long-term persistence than sinks and are prioritized for conservation (Crowder et al. 2000); however, sinks can also make important contributions to regional persistence (Heinrichs et al. 2015; Furrer and Pasinelli 2016). Given the potential for ineffective management outcomes based on approaches that simplify complex spatial dynamics (e.g., local density, abundance (Kanda et al. 2009; Furrer and Pasinelli 2016; but see Heinrichs et al. 2018), systems with putative sources and sinks require rigorously assessments to

evaluate source-sink dynamics and evaluate the contributions of local populations to conservation objectives (Crowder et al. 2000; Loreau et al. 2013). However, source-sink assessments based on demography and movement require intensive data collection to establish a source-sink baseline condition. Additional data is required to further evaluate the impacts of directional change on spatial population dynamics (Breininger and Carter 2003; Heinrichs et al. 2018), making it difficult to anticipate the consequences of management actions and land-use change. Hence, we have a limited understanding of the kinds of events or changes that can de-stabilize or re-organize source-sink dynamics, and the potential magnitudes of such changes.

An understanding of when and how source-sink dynamics could change can support adaptive management strategies for source-sink populations and guide future data collection decisions. If source-sink evaluations are relatively sensitive to change, re-assessments may be required after certain kinds or magnitudes of landscape or population change. If source-sink dynamics are robust to change, a one-time assessment may be all that is needed to guide future decisions under a wide range of conditions. Given the level of investment required to assess sources and sinks with demography and movement (Runge et al. 2006; Furrer and Pasinelli 2016), an indication of the ability of sources and sinks to withstand directional system changes can help gauge an appropriate ‘expiry’ for assessments based on current conditions.

Previous research has identified key factors driving the structure and strength of source-sink dynamics including local patch quality and abundance, network configuration, and movement exchanges (e.g., Heinrichs et al. 2015, 2016) in stationary environments; however, we know little about the influences of directional change on source-sink dynamics. The magnitude, extent, and type of system change, combined with system-specific factors, may determine the degree to which source-sink dynamics is altered. To explore how future management actions and land-use change could alter source-sink dynamics and regional population outcomes, we constructed a simulation analog of a Black-capped vireo source-sink population. We used empirically-based simulation modeling to contrast population outcomes among different scenarios of future change, including habitat loss,

habitat restoration, parasitism control, and changes in movement rates.

Case study

The Black-capped vireo (*Vireo atricapilla*; hereafter also ‘vireo’) is a migratory songbird with breeding populations in central Texas as well as parts of Mexico and Oklahoma. It is threatened by nest parasitism by the widespread Brown-headed cowbird (*Molothrus ater*; cowbird; Ratzlaff 1987), as well as rangeland expansion, forest succession, and land-use change (Wilkins et al. 2006). After the vireo was listed as an endangered species (U.S. Endangered Species Act), cowbird control was enacted and the largest known breeding population increased (Eckrich et al. 1999; Fort Hood; Cimprich and Kostecke 2006).

The Fort Hood military base (~ 90,000 ha) in Texas (Fig. 1; hereafter ‘Fort Hood’) contains seven vireo monitoring sites wherein habitat use, territory mapping, and mark and re-sight data have been collected. Four of these sites represent higher quality vireo habitat (East Range—ER, West Fort Hood—WF, Manning 2—M2, Jack Mountain—JM; Kostecke and Cimprich 2008; 1997–2006) with long time-series of data (> 10 years). Lower quality sites (Maxdale—MX, Taylor Valley—TV, West Range—WR; 2011–2014) were intensively studied over a shorter, four-year period (Walker et al. 2016). Fort Hood includes the majority of vireos in the study population, with off-base populations separated by more than 30 km (mean 60 km) of largely inhospitable matrix. Although areas of Fort Hood function as population sources (Heinrichs et al. 2015; Walker et al. 2016), the population is reliant on the continued trapping and shooting of cowbirds (Wilsey et al. 2014). Other areas on the base function as population sinks, including the majority of the lower quality study areas (Heinrichs et al. 2015; Walker et al. 2016).

Beyond Fort Hood, we evaluated five much smaller populations (Balcones Canyonlands National Wildlife Refuge—BC, San Saba—SS, Colorado Bend State Park—CB, Middle Property—MP, and Goldthwaite—GW) amidst the largely inhospitable matrix of agriculture, rangeland, developed, and urban areas in the surrounding counties. These sites were generally evaluated for the same duration and using the same methods as were the on-base, lower quality sites (Walker et al. 2016). Demographic conditions were

improved by the recent initiation of cowbird control in some off-base populations. However, many of these peripheral areas acted as sink populations through time, and some source-sink classifications changed with inter-annual variability (Walker et al. 2016). Although habitat and population sizes are limited in peripheral populations, they could influence regional population outcomes if they are strong sinks or if movement rates from sources to sinks are high. Movements among on- and off-base populations are poorly understood. Limited banding data (Cimprich et al. 2009; Cimprich, unpublished data; Walker et al. 2016) demonstrate that vireos move among on- and off-base breeding populations and movements among Fort Hood and closer off-base populations may be more common. Yet, the degree to which long-distance dispersal could impact source-sink dynamics and regional population outcomes has not been investigated.

To examine the degree to which source-sink dynamics could change with management and land-use change, we simulated population-specific habitat use, demography, and inter-population movements under alternative scenarios. We explored how source-sink classifications could realistically change with increased off-base cowbird control, habitat expansion near the largest population, the loss of habitats and populations, and increased inter-population movement rates. To make controlled comparisons among scenarios, we assumed consistency in habitat and population factors not related to the change that was being tested. By iteratively removing local populations from the network, we evaluated their contributions to regional population abundance and trajectories (Crowder et al. 2000; Heinrichs et al. 2010). We compared source-sink dynamics among baseline and change scenarios to evaluate the applicability of past source-sink assessments to future source-sink states. We expected source-sink dynamics to be most responsive to scenarios that changed the distribution of resources, by altering habitat amount or configuration. In addition, we expected regional population abundance to be sensitive to changes that affected the largest population, including increased emigration from Fort Hood. By contrast, we expected localized changes to small populations (e.g., increased cowbird control in peripheral populations) to have limited influence on network-wide source-sink dynamics.

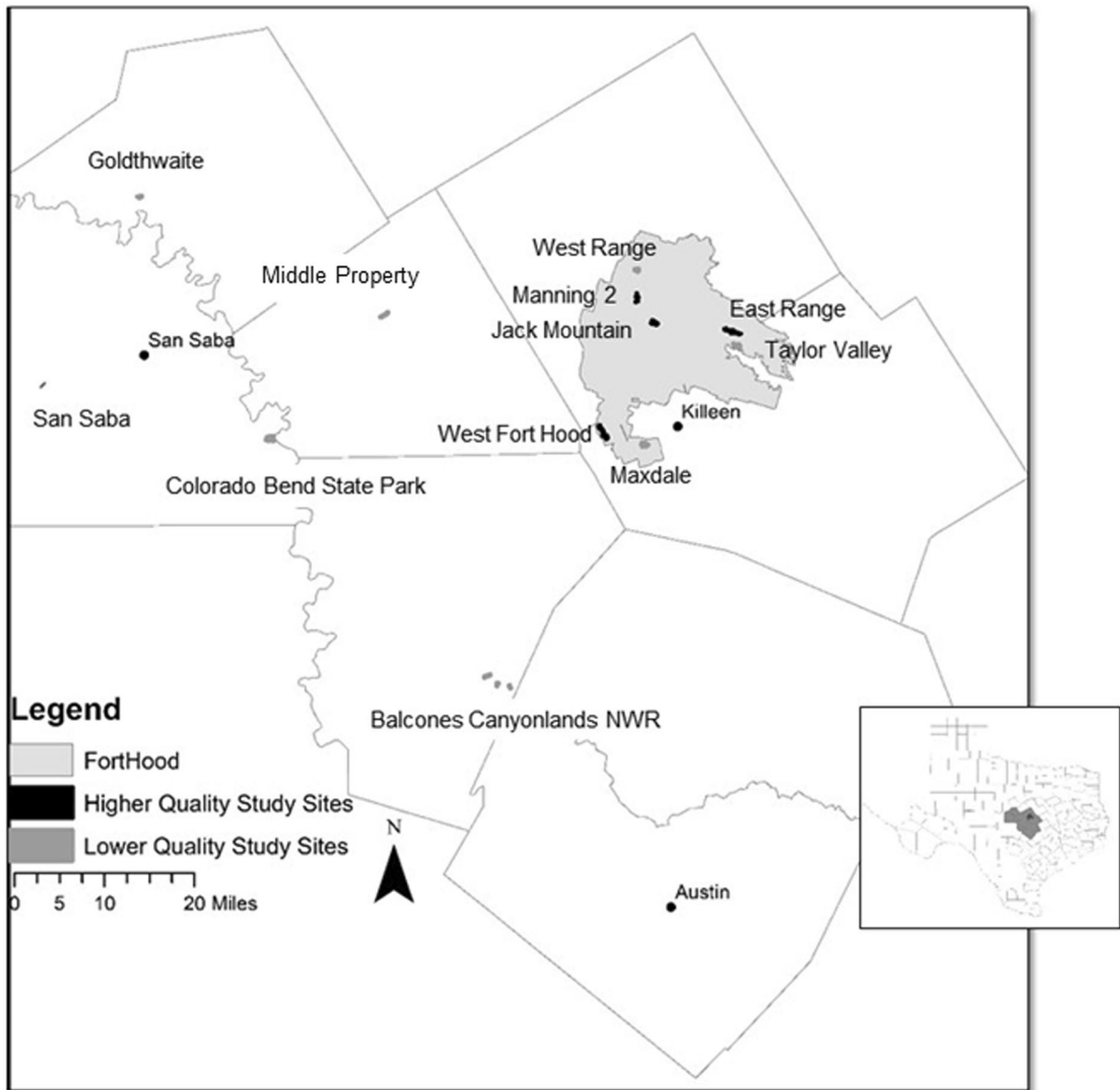


Fig. 1 Black-capped vireo study site locations on and near Fort Hood military base, Texas (adapted from Walker et al. 2016)

Methods

Approach

We used a spatially explicit individual-based modeling framework to construct a simulation model of vireo habitat use, movement, and demography. In this mechanistic model, source-sink dynamics were an emergent function of multiple interacting factors including location-specific habitat conditions, demography, territory sizes and densities, and short- and

long-range movements. Variation in local conditions gave rise to differential population states (i.e., sources and sinks) when summed across local habitats and through time. We used this simulation framework to evaluate both the current and future possible states of this source-sink system using a range of alternative movement, and realistic management, and landscape changes.

Habitat

Black-capped vireos generally breed in patchy shrublands, using areas that vary in structure and species composition (Wilkins et al. 2006; Wilsey et al. 2012). As habitat information differed across our study area, we used a hybrid spatial approach to combine the best available information in each location within a common habitat-population framework. On Fort Hood, we used a continuous habitat suitability model (Wilsey et al. 2012; 75 m pixel resolution) to indicate habitat ‘quality’ throughout the military base. The habitat suitability model used a random forest approach with vireo location data (2002–2003 surveys; Cimprich and Kostecke 2006), remotely sensed vegetation type and height, soil depth, and edge-density maps to estimate the suitability of areas for vireo use (Wilsey et al. 2012; See Appendix). Pixels with habitat suitability probabilities in the upper two tertile bins (i.e., habitat suitability ≥ 0.36) indicated likely habitat (Wilsey et al. 2014), and were used to build exclusive multi-pixel territories. Individuals without territories (hereafter, floaters) could occupy pixels below the suitability threshold but could not establish a territory.

Study populations away from Fort Hood are comparatively small, isolated, and lacked corresponding environmental data (e.g., LiDAR) to replicate on-base habitat models. To delineate habitat from non-habitat (matrix) we created minimum convex polygons (MCP) for each of the sites to encompass mapped territories from 2011 to 2014. These homogeneous habitats within the MCPs were used by simulated individuals to construct territories (see Territory Selection below), that approximated empirical site-specific territory sizes (Table 1). Although there could be small patches of unmapped habitat elsewhere in the landscape, it is unlikely that any larger unidentified and unstudied habitat patches exist.

Population model

We constructed a three-stage habitat-population model using the HexSim modeling platform (Schumaker and Brookes 2018). We focused on modeling males (similar to Wilsey et al. 2014), as adults (in their first or more breeding season) and yearlings (1 year old, in their first breeding season) establish and defend territories that generally include a paired female. Fort

Hood count data and fecundity estimates also reflect successful male territories (Cimprich and Heimbuch 2012) and a males-only model reduced computation time. We also tracked chicks/juveniles (< 1 year old). To begin simulations, we distributed 5478 simulated adult males in habitat according to their 2012 abundance and distribution among sites (Cimprich and Heimbuch 2012). Birds on Fort Hood, but outside of the demographic study sites, were placed in higher suitability pixels and were given multiple opportunities to move and locate a suitable territory, until virtually all had successfully established a territory. After this initialization period, simulated vireos then underwent an annual flow of events including reproduction and survival, territory selection, and juvenile local and long-distance dispersal (Fig. 2).

Movement

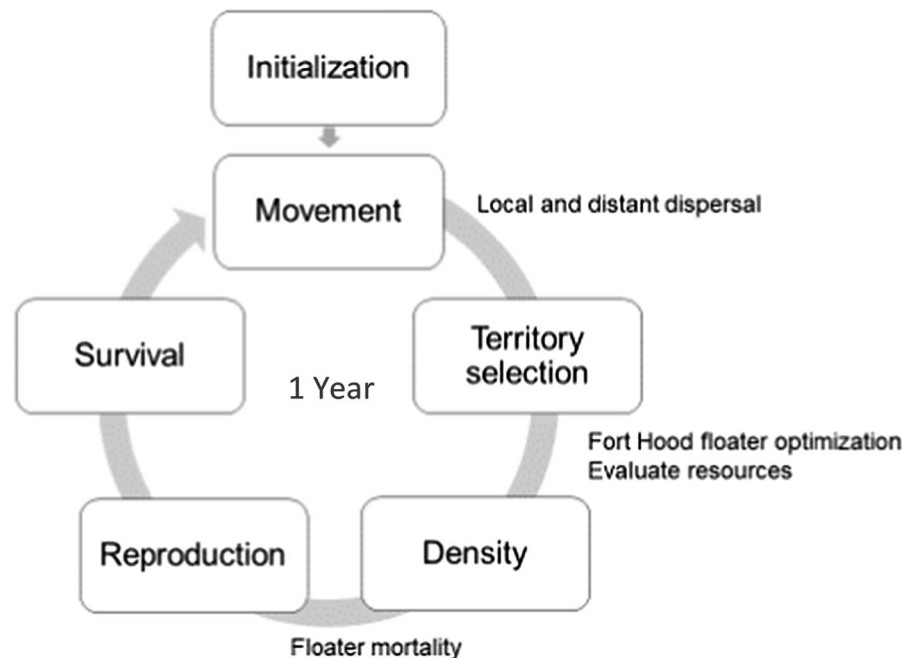
Black-capped vireos migrate from their Texas breeding range to their winter range in Mexico (Graber 1961; Vega Rivera et al. 2011); however, surviving adults often return to the same breeding territory after spring migration (Walker et al. 2016). As our focus was on breeding population dynamics, our model assumed that surviving adults remained on their territories. Similarly, many juvenile black-capped vireos return to their natal area after migration to establish territories a short distance away (Walker et al. 2016). These local juveniles dispersed on Fort Hood by drawing a path length from a uniform distribution with a minimum path length of 3.75 km (50 pixels). Dispersers could move to any location in Fort Hood in search of a suitable territory but stopped moving if they encountered 3 consecutive pixels of habitat after 5.6 km (75 pixels). These minimum movement distance thresholds were experimentally chosen to allow juveniles to exit their natal study site, move away from areas occupied by adults, select a nearby unoccupied territory, and were evaluated against empirical data. Simulated birds were attracted to higher habitat suitability scores (above the habitat threshold) and moved with forward momentum (80% autocorrelation in path direction over the previous 5 pixels). To match these circuitous movement distances with empirical Euclidean displacement distances, we iteratively modified thresholds until simulations matched empirical targets. Using these values, juveniles dispersed a mean distance of 2.5 km from their

Table 1 Territory selection criteria for simulated black-capped vireos across the study area in Texas

Site	Empirical min territory size (ha)	Max. territory size (pixels; ha)	Number of coinciding males (max)	Mean site habitat suitability	Min. territory condition	Explored area (pixels)
SS	0.24	1.0; 0.49	2	1 ^a	1	65
BC	0.44	1.0; 0.49	1	1 ^a	1	275
GW	1.41	2.9; 1.41	1	1 ^a	2	39
TV	0.44	1.0; 0.49	1	44.3	40	144
CB	0.95	2.0; 0.95	1	1 ^a	1	214
MP	2.22	4.6; 2.22	1	1 ^a	4	31
MX	0.60	1.2; 0.60	1	36.0	44	179
WR	0.54	1.1; 0.54	1	61.2	68	121
ER	0.14	1.0; 0.49	3	94.8	27	179
JM	0.28	1.0; 0.49	2	85.8	49	114
M2	0.18	1.0; 0.49	2	90.5	33	95
WF	0.10	1.0; 0.49	5	78.3	16	185
FH	0.3 (min), 0.43 (mean)	1.0; 0.49	1	58.0	17 (min), 51 (target)	179

^aOff-base sites with binary habitat characterizations are indicated by pixel scores of 1

Fig. 2 Order of population and model routines in the annual black-capped vireo model



natal nest to their selected territory, matching natal dispersal records (mean 2.6 km, range 0–30 km, SD = 4.4 km (Cimprich, unpublished data; Walker 2015; Walker et al. 2016), excluding inter-patch distance records, as inter-patch dispersal was conducted separately.

Dispersal events between Fort Hood and off-base breeding sites occur but are rarely observed (Cimprich unpublished data; Cimprich et al. 2009; Walker et al. 2016). As there are few tracked birds relative to the overall population size and only a few years of data collected outside of Fort Hood, the frequency and

patterns of movements among Fort Hood and more distant populations are poorly understood. We used natal dispersal data from 1992 to 2015 and inter-patch distances to infer distance-based rates of exchange among breeding populations. We divided the five inter-patch dispersal records (≥ 30 km, minimum inter-patch distance) by the total number of natal dispersal records (324) to estimate the proportion of vireos dispersing within- (0.985) versus among-patches (0.015). As the recorded inter-patch dispersals were closest to the off-base site (Balcones Canyonlands National Wildlife Refuge), we constructed an inverse distance-based matrix of inter-patch dispersal probabilities to move simulated birds from one breeding population to another. Alternative inter-patch movement probabilities were also evaluated (see movement scenarios below) to assess the sensitivity of model outcomes to movement rates.

Territory selection

After moving, simulated birds first explored their surrounding area to assess their territory options (see Table 1 for search radii). Individuals occupying on- and off-base study sites explored an area equivalent to their entire study site (0.31–1.34 km²; Fig. 5—red and orange; Appendix) in search of available territories. Similarly, birds on Fort Hood but outside of demographic study sites, explored an equivalent area (e.g., radius of 0.5 km; Fig. 5—white, gray; Appendix) for prospective territories.

Individuals then selected the best unoccupied territory within their search range using site-specific territory size and selection criteria, reflecting measured differences in habitat (e.g., variable suitability on Fort Hood) and population conditions (e.g., territory sizes) in each location. To account for the partial overlap of male territories, we used the minimum empirical territory sizes (as measured by Walker 2015; Walker et al. 2016; see Table 1) to describe the maximum extent of non-overlapping territories. Optimal territories contained the highest level of resources, as determined by the size of the territory (number of available continuous pixels) multiplied by the habitat suitability scores of the pixels (on-base only; off-base suitability was uniform). Territories were required to meet a minimum territory condition (minimum territory size * mean site suitability; Table 1) using a up to a maximum number of contiguous pixels (max.

territory size; Table 1) to limit the area that an individual could defend. Where minimum empirical territory sizes (as measured by Walker 2015; Walker et al. 2016; see Table 1) were smaller than a single pixel, we allowed more than 1 male to occupy a territory to overcome pixel size limitations and maintain expected population densities (maximum number of coinciding males; Table 1). Individuals outside of the study areas on Fort Hood that were unable to find a suitable territory (i.e., floaters) on their first try were given additional short movement and territory-selection opportunities (up to 150 repeated attempts before the breeding season) to ensure that simulated birds could occupy proximate suitable territories before a 50% mortality penalty was applied to birds without territories. The number and locations of territories were dynamic among years as territories were specific to individuals.

Reproduction

Simulated birds drew a location-specific probability (Table 2) of having a successful territory from a Bernoulli distribution (annually, with replacement) using site-specific empirical territory success probabilities (Walker 2015; Walker et al. 2016). We defined successful territories as those that produced at least one fledgling through one or more broods in a given year.

Birds with successful territories drew a number of male fledglings (assuming an equal sex ratio at birth) from a Bernoulli distribution, based on the mean and variance in the number of fledglings per total successful territory in a given site (Table 2). Simulated birds outside of the demographic study areas on Fort Hood were assigned interpolated territory success and a number of fledglings based on the resource condition of their territory. Site-specific habitat suitability values were used to fit a linear relationship to predict territory success and number of fledglings in lower quality habitats (up to mean suitability values of 0.44, and 0.61 respectively), where an increasing relationship with higher habitat suitability pixels was evident. Habitats similar to higher suitability study sites were assigned the mean territory success rates and mean number of fledglings of high quality study sites. Site-specific territory success and fledgling data from 2005 to 2015 were used for on-base study sites ER, JM, M2, WF (Cimprich, unpublished data), and

Table 2 Black-capped vireo territory success and number of fledglings assigned to simulated birds, based on their location within a study site or resource condition of their territory (Fort Hood)

Site	Territory success Mean	Territory success SD	Male fledglings/successful territory	Adult survival mean; (SE)
SS	0.54	0.33	1.98	0.52 (0.05)
BC	0.46	0.16	1.50	0.36 (0.05)
GW	0.54	0.28	1.79	0.46 (0.14)
ER	0.64	0.14	1.78	0.33 (0.04)
CB	0.34	0.14	1.70	0.46 (0.05)
MP	0.29	0.23	1.25	0.45 (0.07)
MX	0.43	0.10	1.52	0.41 (0.04)
WR	0.69	0.13	1.77	0.35 (0.04)
ER	0.62	0.12	1.66	0.37 (0.03)
JM	0.53	0.07	1.76	0.27 (0.04)
M2	0.74	0.13	1.80	0.54 (0.03)
WF	0.63	0.13	1.69	0.44 (0.04)
FH	0.43–0.64	0.12	1.52–1.79	0.41 (0.04)

2011 to 2014 for lower quality on-base sites (TV, MX, and WR) and off-base study sites (Walker 2015; Walker et al. 2016).

Survival

The annual survival of adult vireos on Fort Hood differed among study sites (Kostecke and Cimprich 2008; Walker et al. 2016) and simulated birds drew the corresponding empirical survival rates measured at their site from a truncated normal distribution. As a robust relationship between habitat suitability values and adult survival rates on Fort Hood was not evident, individuals outside of the study sites were given a mean survival rate that averaged survival across all Fort Hood study sites (based on combined estimates for all on-base sites excluding JM; Walker et al. 2016). For all life stages, empirical means and variances were used to create site-specific normal distributions, from which survival rates were drawn each year. Limited data precluded the assessment of adult survival correlation among populations through space and time. We assumed that within a population, factors influencing fluctuations in survival were correlated (1.0; e.g., on Fort Hood) and uncorrelated among distant populations (0.0; between Fort Hood and all peripheral populations) that were separated by long distances of non-habitat. Juvenile (young of the year)

survival was defined as the probability of a vireo banded as a nestling surviving and returning to a study site following migration (Walker et al. 2016). Because natal resighting probabilities were low (< 2.6% of males) and confidence intervals of estimates were large, we explored two alternative hatcher survival rates (in alternative simulation scenarios) to account for possible under-estimates of survival resulting from incomplete site fidelity (Cilimburg et al. 2002; Kostecke and Cimprich 2008). We simulated population dynamics using the empirically-estimated hatcher survival rate (0.46 ± 0.07 ; Walker et al. 2016), as well as a higher rate of 0.54 (SE = 0.07; within the 95% CI), chosen to produce a largely stable population and approximate the range of abundance estimates from 2005 to 2015 (Cimprich and Heimbuch 2011, 2012; Cimprich, unpublished data). Each year, a hatcher survival rate was drawn from the normal distribution and applied to hatchers in all locations as site-specific estimates were not available.

Simulations

Baseline simulation: We simulated population dynamics for the region over 50 years, and summarized population outcomes across 25 replicate simulations. In addition to assessing location-specific population sizes through time, we also tracked individual births,

deaths, immigration, and emigration through space. We evaluated two source-sink metrics: (1) Productivity (births – deaths), and BIDE (births + immigration) – (deaths + emigration), tallied for each study site (off-base) and each pixel on Fort Hood. Sources were indicated by positive source-sink metric values. Negative values indicated sinks.

Movement scenarios: To assess the impact of juvenile dispersal on source-sink outcomes, we implemented alternative rates of exchange among discrete breeding populations. We assumed that empirical estimates underestimated exchanges of birds and evaluated scenarios with higher proportions (three or ten times) of juvenile dispersal. We also evaluated a no inter-population movement scenario (Table 3).

Habitat loss scenarios: To evaluate which areas have the largest effect on source-sink dynamics, we iteratively removed study sites representing the strongest source and sink populations as indicated by the BIDE metric. We also evaluated the source-sink status of off-base study sites in the absence of Fort Hood as it is the primary source of inter-population dispersers.

Cowbird control scenario: Nest parasitizing cowbirds are controlled using trapping and/or shooting in the majority of habitat on Fort Hood (excepting West Range and surrounding area) to improve black-capped vireo fecundity and persistence. Cowbird control efforts in peripheral populations (BC: 2011–2014) have also been recently initiated (e.g., 2013 or 2014 in CB, SS) but the intensity of control varies among sites. To examine how further increases in off-base cowbird

control could affect source-sink dynamics, we simulated the impact of increased cowbird control effort on territory success and number of fledglings. We quantified the difference in territory success and fledglings before versus after the implementation of cowbird control at off-base sites and used this difference to indicate the degree to which increased cowbird control intensity could further improve reproductive success. To do so, we averaged annual measures of reproductive success before cowbird control (CB in 2012 and SS sites from 2012 to 2013, respectively), subtracted these from post-control (2014) values, and averaged the resulting differences among sites. This resulted in a mean 0.28 increase in territory success, and 0.24 increase in the number of males fledged from successful territories.

Habitat restoration scenarios: To examine the degree to which peripheral (off-base) habitat restoration actions could change regional source-sink dynamics, we digitally expanded and restored possible vireo habitats and simulated emergent source-sink dynamics. We identified public lands in the counties of study populations that: (1) were composed of likely vireo habitat types including deciduous, coniferous, mixed forest, or shrub vegetation classes (NLCD 2011; USGS 2011), (2) were at least 15 ha in size (Fig. 6—blue; Appendix), (3) and excluded extreme topographical features. New sites were assumed to be uniformly suitable (as for other off-base sites) due to habitat data constraints. Simulations began with an additional 100 males randomly distributed among new habitats. In alternative scenarios, we restored habitats

Table 3 Management action and land-use change scenarios simulated for Black-capped vireos in Texas

Scenario	Change	Scenario description
Baseline	n/a	Status quo; higher hatcher survival rate
Low hatcher survival	Survival	Hatcher survival using the empirical mean value
No movement	Movement	No inter-population movement (on–off base; off–off base)
Movement 3 ×	Movement	Three times higher inter-population movement frequencies
Movement 10 ×	Movement	Ten times higher inter-population movement frequencies
Fort hood removed	Habitat loss	All habitat on Fort Hood is replaced with matrix
M2 removed	Habitat loss	Manning 2 habitat (on-base) replaced with matrix
ER removed	Habitat loss	East range habitat (on-base) replaced with matrix
MP removed	Habitat loss	Middle property (off-base) habitat replaced with matrix
Increased cowbird control	Reproduction	Increased territory success and number of fledglings in off-base sites
Habitat restoration	Habitat restoration	Restored possible vireo habitats to allow occupancy

to sink- and source-like demographic conditions. To approximate partial habitat restoration that allowed occupancy but sub-optimal demography with limited or no cowbird control, we parameterized territory sizes, territory success, and adult survival to be equivalent to those measured for the Balcones sink population. Territory success and adult survival rate distribution means were each increased by 0.2 to allow restored habitat to function as population sources, as might be achieved by a complete restoration effort that included intensive cowbird control. Distance-based dispersal patterns were updated to include restored patches, re-distributing the static proportion of long-distance dispersers among new and existing patches. Population dynamics for all management and land-use scenarios were simulated for 50 years and results from 25 replications were averaged. To facilitate comparisons among field and model-based approaches to assessing source-sink dynamics, we calculated source-sink states at the beginning of simulations using a comparable 5-year data series. To assess long-term source-sink performance, we re-calculated source-sink states using population conditions at the end of the simulation (years 45–50).

Results

Baseline abundance and source-sink dynamics

The population was relatively stable but declining over the fifty-year period in the baseline scenario that used elevated hatcher survival rates. The population size was within the range of variation observed from 2005 to 2012 and resulted in a final population size that exceeded observed abundance in some years (e.g., 2008 and 2011). This baseline scenario (using higher hatcher rates) better represented past abundance estimates whereas mean hatcher survival rates resulted in a strong declining trend and population sizes that were well below recent population estimates (Fig. 3). Hence, higher hatcher rates were used as the basis for all source-sink scenarios. The majority of sites functioned as sinks, with few sources (Productivity and BIDE metrics; Table 4). MP and BC acted as the strongest off-base breeding population sinks. Fort Hood and M2 emerged as the strongest sources, and WR and WF functioned as weaker on-base sources

during early (years 5–10) or late (years 45–50) evaluation periods.

Habitat loss

To evaluate the loss of key sources and sinks on regional population abundance and the stability of source-sink classifications, we iteratively removed strong source (FH, M2), weak sink (ER) and strong sink (MP) patches. The removal of Fort Hood and all on-base habitat resulted in regional population declines to near-extinction. In the absence of this central habitat, one weak peripheral sink (SS) became a source indicating a pseudo-sink that changed status with altered movement and densities. The remaining sinks were weaker as a result of lower abundance. The removal of the strongest on-base source, M2, had little effect on the ending regional population size relative to the baseline (Fig. 4b). However, its removal caused a proximate weak source to become a sink (WR; Table 5), indicating that some populations have strong dependencies. The removal of this small strong source also reduced the source strength of the general Fort Hood area to 1/16 of baseline conditions (Table 5).

Removing a weak central sink (ER; on-base study site) lessened long-term abundance and diminished the strength of source-sink dynamics, but to a lesser extent than removing the strong sink (M2). The loss of ER similarly caused the proximate weak source (WR) to become a sink. Removing a strong peripheral sink (MP; off-base) had the largest effect on end-abundance (excepting Fort Hood) and lessened the strength of source-sink dynamics (Table 5). However, the removal had no effect on the source-sink status of breeding populations.

Movement

The degree to which breeding populations exchanged juveniles via long-distance dispersal impacted regional population outcomes. When we tripled the proportion of juveniles moving among breeding populations, mean population sizes were substantively lower. With ten times higher inter-population dispersal, abundance approximated that of the low hatcher survival scenario, offsetting the increased juvenile survival of the baseline scenario (Fig. 3). Limiting movement among populations increased abundance relative to scenarios with higher movement rates.

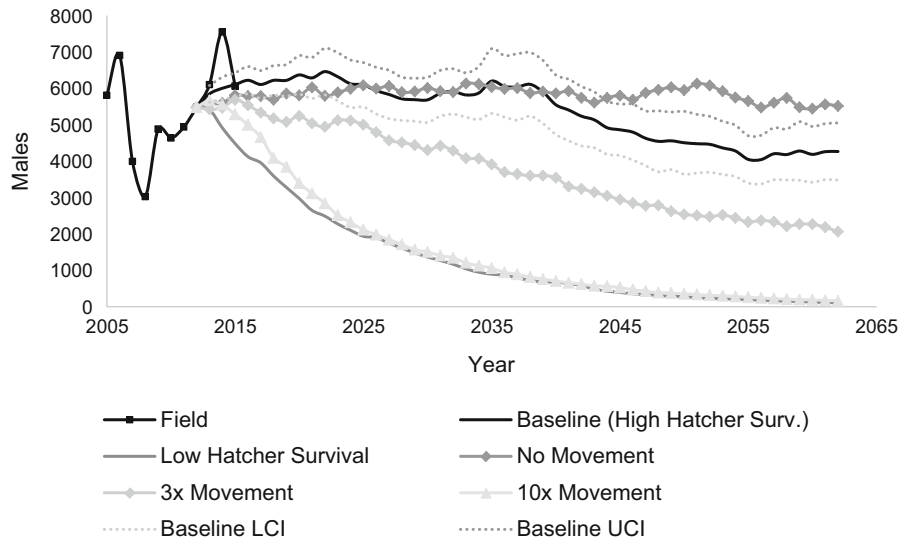


Fig. 3 Simulated mean Black-capped vireo abundance under baseline and alternative scenarios relative to field abundance estimates (averaged over 25 replications), using both mean hatcher survival (lower hatcher survival scenario) and increased hatcher survival rates (baseline scenario), and alternative rates

of movement among Fort Hood and peripheral populations. Lines indicate male abundance, averaged among all replicates. Dashed lines indicate the 95% upper and lower confidence intervals around mean baseline abundance through time

Table 4 Simulated black-capped vireo source-sink dynamics using lower hatcher survival rates and higher hatcher survival rates (baseline scenario). Source-sink dynamics were characterized using productivity and BIDE metrics during the first and last years of simulations. Sources (in bold) are indicated by positive metric values, sinks by negative values

Site	Baseline Years 5–10		Baseline Years 45–50	
	Prod.	BIDE	Prod.	BIDE
SS	- 124	- 488	- 86	- 261
BC	- 1333	- 2508	- 1255	- 2062
GW	- 1147	- 1469	- 798	- 1072
CB	- 1250	- 2279	- 963	- 1686
TV	- 87	- 14	- 40	- 89
MP	- 2145	- 2364	- 1573	- 1737
MX	- 48	- 68	- 39	- 48
WR	- 22	- 21	14	23
ER	- 175	- 129	- 61	- 46
JM	- 296	- 306	- 261	- 325
M2	705	1259	471	647
WF	80	284	3	31
FH	14,064	16,905	11,231	13,747

Source-sink dynamics are characterized using productivity and BIDE metrics during the first and last years of simulations. Sources (in bold) are indicated by positive metric values, sinks by negative values

In scenarios with higher inter-population movement rates, movement changes affected abundance more than they affected source-sink dynamics. With fewer individuals in the population, source-sink strength was universally diminished; however, source-sink classifications were unaffected (Table 5). Tripled movement frequencies (i.e., three times more dispersal than baseline conditions) reduced regional abundance to a lesser extent than the ten times scenario. Although the source-sink strength of many on-base sites was reduced, the strength of peripheral populations increased.

Cowbird control

When cowbird control was increased on all off-base sites, improvements in territory success and number of fledglings transformed most sinks (San Saba, weak sink; Balcones, strong sink; and Colorado Bend, strong sink) into sources (Table 4). However, the distant GW and central MP populations remained sinks. Despite substantive improvements for off-base breeding populations, increased cowbird control in these small populations did not yield improvements in regional abundance (Fig. 7; Appendix).

Fig. 4 The effect of source and sink removals on simulated Black-capped vireo, **a** population trajectories, relative to field estimates and baseline predictions and **b** mean population sizes over the last 10 years of simulations. Dashed lines indicate the 95% upper and lower confidence intervals around mean baseline abundance through time

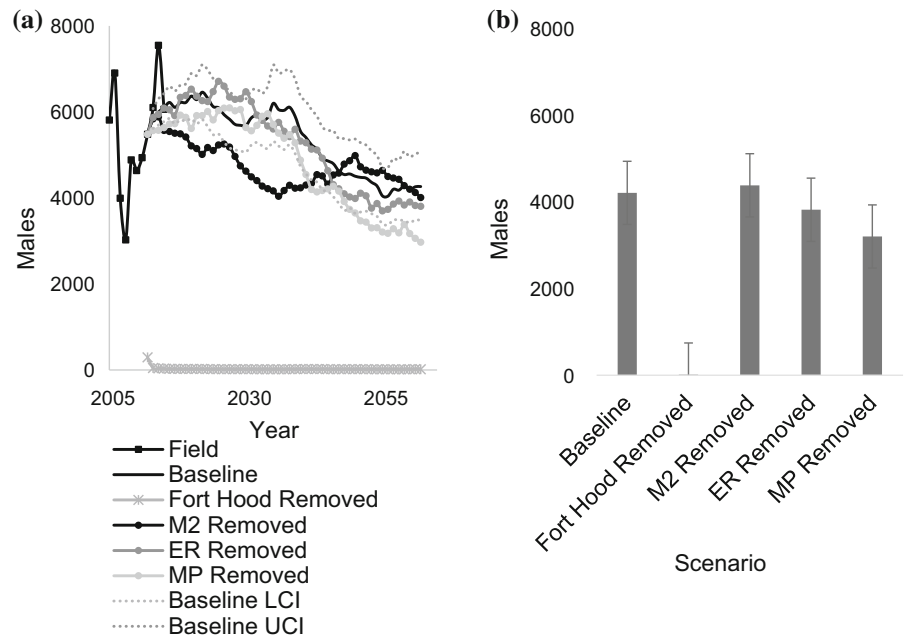


Table 5 Source-sink status and strength of breeding Black-capped vireo populations under alternative habitat removal and inter-population dispersal scenarios, as characterized by positive (source, in bold) or negative (sink) BIDE values (years 45–50)

	No M2	No MP	No ER	No FH	3 × Dispersal	10 × Dispersal	Baseline
SS	- 146	- 166	- 236	299	- 763	- 106	- 261
BC	- 1503	- 1864	- 1196	- 2	- 2881	- 734	- 2062
GW	- 919	- 1126	- 709	- 14	- 1705	- 442	- 1072
CB	- 1410	- 1940	- 1036	- 6	- 2792	- 745	- 1686
TV	- 15	- 55	- 53	N/A	28	- 9	- 89
MP	- 1397	N/A	- 1056	- 8	- 2755	- 792	- 1737
MX	- 25	- 45	- 17	N/A	- 43	- 27	- 48
WR	- 70	10	- 45	N/A	63	1	23
ER	- 162	- 82	N/A	N/A	- 57	- 19	- 46
JM	- 222	- 229	- 169	N/A	- 173	- 12	- 325
M2	N/A	549	359	N/A	462	70	647
WF	12	7	14	N/A	25	8	31
FH	856	1280	8917	N/A	4709	1202	13,747

Habitat restoration

Creating new habitats by restoring suboptimal public lands (Fig. 6; Appendix) to peripheral sink population conditions (BC; closest population to the majority of new habitat) caused a decline in regional abundance and restored habitats generally acted as population sinks (Table 6). However, if habitats were fully restored to conditions that supported higher territory success and survival rates, restored habitats functioned as strong sources and regional abundance increased.

Discussion

Forecasting the impacts of management and land-use change is important in planning effective conservation actions for species at risk of decline. We predicted the degree to which different types of changes could alter source-sink dynamics and population outcomes. Our black-capped vireo case study highlighted that the stability of source-sink dynamics can depend on the magnitude and location of change as well as the type of change.

Table 6 Source-sink status and strength of breeding Black-capped vireo populations under alternative off-base cowbird control and habitat restoration scenarios, as characterized by

(source, in bold) or negative (sink) BIDE values (years 45–50) and combining 25 simulation replicates

Site	Increased cowbird control	Habitat restoration (sink conditions)	Habitat restoration (source conditions)	Baseline
SS	594	– 183	– 925	– 261
BC	497	– 218	– 2270	– 2062
GW	– 850	– 428.5	– 920	– 1072
CB	187	– 327.5	– 8220	– 1686
TV	– 26	– 168.5	– 235	– 89
MP	– 1417	– 676	– 1490	– 1737
MX	– 52	– 176.5	– 910	– 48
WR	33	34.5	– 60	23
ER	– 132	– 87	– 110	– 46
JM	– 226	– 215.5	– 580	– 325
M2	598	449	1040	647
WF	24	– 48	– 170	31
FH	5721	146	8355	13,747
		Restored: – 3980	Restored: 183,050	

Structural system changes

Population responses to habitat removals revealed the degree of inter-dependency among breeding sites and the contribution of individual sites to regional abundance. As expected, the removal of the largest population and strongest source had the greatest effect on population outcomes and source-sink dynamics. The finding underscores the importance of Fort Hood for regional persistence and demonstrates the dependency of distant populations on this stronghold. By contrast, removing small individual study sites (i.e., strong sources or sinks) had a much smaller effect on regional abundance and source-sink dynamics. Although source-sink strengths changed, site-specific source or sink status remained largely stable. This suggests that management actions that target sources and sinks based on pre-change source-sink assessments are likely to be valid following minor habitat loss and similar changes to the network. However, these and other conclusions assume that beyond the element that was changed (e.g., removal of small habitats and changes to dependent processes), other system elements remain intact and the measured demographic rates, life history, behaviors etc., continue. Although this design allows us to make conclusions about the relative influence of each

change factor, populations and habitats often change in many ways. For example, a minor loss of habitat coupled with habitat degradation (affecting demography) elsewhere could change population dynamics and source-sink structure. Management decisions should assess whether multiple types of change need to be considered in evaluating the stability of past source-sink assessments.

Adding extensive off-base habitat had variable influences on regional population abundance and source-sink dynamics. Partially restoring habitat to sink-like conditions did not improve vireo abundance through time and weakened previously strong and central sources. As restored habitats were close to the central source, simulated vireos moved from Fort Hood to new habitats with higher probabilities than more distant sites. Increased movement to population sinks weakened the strong source population and reduced regional abundance. By contrast, fully restoring habitats and intensively controlling cowbirds to improve demographic rates (territory success and survival) created strong sources that increased regional abundance. Habitat restoration efforts with adequate vegetation structure and composition, coupled with intensive cowbird control could provide an effective means of increasing vireo abundance and distribution. However, as it is difficult to pre-

determine the suite of conditions required to create high quality habitat, population performance in restored habitats should be monitored to ensure that habitat improvements result in source rather than sink conditions. Extensive restoration efforts and similar large-scale changes likely require the re-assessment of sources-sink dynamics to characterize new movement patterns and rates, inter-dependencies, re-identify sources, sinks, and their strengths, and make appropriate future management decisions. Smaller restoration projects are less likely to impact regional dynamics, and source-sink re-assessments may not be required beyond the restored habitat and its primary dependent populations.

Demographic and movement changes

Increased off-base cowbird control affected peripheral source-sink strength and status, with improvements in territory success and number of fledglings weakening strong sinks or causing sinks to become sources. Despite local improvements, increased cowbird control in the small peripheral populations had minimal impact on regional abundance as improvements influenced only a small proportion of the population. However, increased cowbird control in small peripheral or restored sites may be an important means of creating sources and increasing population redundancy across central Texas. Improvements to peripheral sinks may also be an important objective if long-distance dispersals are more frequent than assumed in our baseline conditions.

By contrast, increased inter-population movements had little effect on source-sink status but reduced regional abundance. This supports the findings of source-sink studies where emigration was detrimental to the migrating individuals (Morris 2011), diminishing the regional population, but contrary to other theoretical findings (Franco and Ruiz-Herrera 2015). By virtue of Fort Hood's large population size, inter-population movement flows were primarily from Fort Hood to peripheral sink populations and the redistribution of juveniles to suboptimal locations resulted in a greater number of deaths in off-base sites. Our results indicate that actions aimed at increasing the dispersal to peripheral populations may be detrimental to regional persistence when peripheral sites are sink populations and territory site fidelity is high. As one of the most influential

uncertainties was the frequency of inter-population dispersal events, better information characterizing the rates and patterns of vireo movement is important for effectively prescribing regional management actions. Further, a mechanistic understanding of the factors that influence inter-patch dispersal is lacking but integral to improving and predicting movement responses to management and land-use change.

Source-sink signals

Source-sink signals transcended different methods of estimation and stochastic noise, affording greater confidence in managing populations based on source-sink signals. Source-sink modeling results largely agreed with field-based classifications from previous studies (Walker et al. 2016), with both approaches classifying the peripheral Balcones, Colorado Bend, and Goldthwaite sites as sinks, as well as the central Maxdale and Jack Mountain populations as long-term sinks. Both classified Manning 2 and West Fort Hood as sources and there was agreement on West Range when simulations evaluated a comparable period (years 5–10).

Yet, other source-sink signals can be a product of transient environmental conditions, influenced by analysis or modeling constructs, or affected by directional change. For example, source-sink evaluations (comparing years 5–10 and 45–50) indicated the potential ability of some sites to transition from weak sinks to weak sources within the same scenario. Disagreements in source-sink status also resulted from different assessment methods (San Saba and Taylor Valley; assessed as sources by field data and weak sinks using simulation). Field-based evaluations used survival and fecundity data in stochastic matrix models but did not consider inter-population movements due data constraints (see Appendix). By contrast, our simulation modeling approach explicitly considered emigration and immigration in source-sink calculations and evaluated source-sink dynamics through broader spatial and temporal extents. Both approaches evaluated transient source-sink behavior among years but also generalized source-sink states - through time. Simulated source-sink predictions were the product of several stochastic simulation repetitions and included a more comprehensive range of population conditions than experienced during recent field data collection and used in stochastic growth rate

calculations. The simulation model also included additional data describing habitat, territory sizes, and territory success to represent the influences of source-sink dynamics throughout Fort Hood on regional population dynamics. Whether caused by variability, directional change, or data limitations, populations with weaker source-sink signals may require additional monitoring and analysis to understand the factors driving local population dynamics and design appropriate long-term management strategies.

System stability

Directional system changes can differentially affect source-sink status and regional population abundance. Some factors that led to only minor changes in source-sink status precipitated large changes in regional abundance. In this system, source-sink status was affected more by changes in habitat and population patterns rather than pattern-preserving changes in movement rates. This indicates that management actions or land-use changes that alter local demographic conditions (e.g., off-base cowbird control), movement patterns (e.g., change the network spatial structure), or large habitat changes are likely to require the re-evaluation of source-sink dynamics. By contrast, regional abundance was more responsive to the magnitude of system change than the pattern of change. For example, regional abundance was much more sensitive to changes in the proportion of birds emigrating from Fort Hood (92–100% of patches retained their source or sink status) than changes affecting regional movement patterns (46–77% of patches preserving their source-sink status). This suggests that management actions based on pre-change source-sink classifications are likely to be robust to small habitat or population modifications and small-moderate spatially homogenous changes. As the intensity and pattern of change can differentially affect source-sink status and regional population abundance, joint consideration of these factors is required to anticipate the impacts of change on source-sink systems. Uncertainty analyses, such as undertaken here, can help gauge the degree of expected change, highlight additional data needs, and point to relevant conservation actions in changing source-sink systems.

This case study demonstrates that important interdependencies within a population network can influence the success of management and conservation

actions, even in systems with highly asymmetrical population sizes. Large shifts in source-sink dynamics or abundance occurred in some scenarios of landscape change, indicating the potential for adverse consequences if spatial population structure is not considered e.g., adding large sink habitats weakened key sources and reduced regional abundance. Yet accurately classifying sources and sinks is challenging, particularly in variable and directionally changing systems. Our example illustrates that the stability of source-sink classifications depends on the type, intensity, and pattern of management and land-use change. Changes that largely preserve the pattern of habitat and demographic conditions may require less frequent re-assessments than those with pattern-altering changes. By contrast, large structural changes are more likely to require re-evaluation of source-sink dynamics to support effective management actions. Hence, decisions of which sources and sinks to protect or alter are best informed by the simultaneous consideration of source-sink dynamics (Weegman et al. 2016), abundance, and the type of management and land-use change. This example highlights the importance of understanding source-sink dynamics for the successful management of at-risk populations as well as the need for the continued development of source-sink theory, methods, and best practices that target species at risk in complex and changing landscapes.

Acknowledgements We thank John Marzluff and Chad Wilsey for input and useful discussions.

Funding Funding was provided by Strategic Environmental Research and Development Program (SERDP) as part of project RC-2120. The content of this manuscript does not necessarily reflect the position or policy of the United States government and no official endorsement should be inferred.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

References

- Bancroft BA, Lawler JJ, Schumaker NH (2016) Weighing the relative potential impacts of climate change and land-use change on an endangered bird. *Ecol Evol* 6:4468–4477

- Breining DR, Carter GM (2003) Territory quality transitions and source-sink dynamics in a Florida scrub-jay population. *Ecol Appl* 13:516–529
- Cilimburg AB, Lindberg MS, Tewksbury JJ, Hejl SJ (2002) Effects of dispersal on survival probability of adult yellow warblers (*Dendroica Petechia*). *Auk* 119:778–789
- Cimprich DA, Heimbuch M (2011) Monitoring of the Black-capped vireo during 2011 on Fort Hood, Texas. Endangered Species Monitoring and Management at Fort Hood, Texas: 2011 Annual Report. Natural and Cultural Resources Management Branch. Fort Hood
- Cimprich DA, Heimbuch M (2012) Monitoring of the Black-capped vireo during 2012 on Fort Hood, Texas. Endangered Species Monitoring and Management at Fort Hood, Texas: 2012 Annual Report. Natural and Cultural Resources Management Branch. Fort Hood
- Cimprich DA, Kostecke RM (2006) Distribution of the black-capped vireo at Fort Hood, Texas. *Southwest Nat* 51:94–102
- Cimprich DA, Sexton CW, McDowell PK, Lasley G, Simper WS (2009) Long-distance dispersal records for the Black-capped vireo. *Bull Tex Ornithol Soc* 42:44–47
- Copeland HE, Doherty KE, Naugle DE, Pocewicz A, Kiesecker JM (2009) Mapping Oil and gas development potential in the US intermountain west and estimating impacts to species. *Plos One* 4:e7400
- Crowder LB, Lyman SJ, Figueira WF, Priddy J (2000) Source-sink population dynamics and the problems of siting marine reserves. *Bull Mar Sci* 66:799–820
- Eckrich GH, Koloszar JA, Goering MD (1999) Effective landscape management of brown-headed cowbirds at Fort Hood, Texas. *Stud Avian Biol* 18:267–274
- Franco D, Ruiz-Herrera A (2015) To connect or not to connect isolated patches. *J Theor Biol* 370:72–80
- Furrer RD, Pasinelli G (2016) Empirical evidence for source—sink populations: a review on occurrence, assessments and implications. *Biol Rev* 91:782–795
- Graber JW (1961) Habitat requirements and life history of the black-capped vireo (*Vireo atricapilla*). *Ecol Monogr* 31:313–336
- Hannah L, Midgley GF, Millar D (2002) Climate change-integrated conservation strategies. *Glob Ecol Biogeogr* 11:485–495
- Heinrichs JA, Bender DJ, Gummer DL, Schumaker NH (2010) Assessing critical habitat: evaluating the relative contribution of habitats to population persistence. *Biol Conserv* 143(9):2229–2237
- Heinrichs JA, Lawler JJ, Schumaker NH, Wilsey CB, Bender DJ (2015) Divergence in sink contributions to population persistence. *Conserv Biol*. <https://doi.org/10.1111/cobi.12540>
- Heinrichs JA, Lawler JJ, Schumaker NH (2016) Intrinsic and extrinsic drivers of source-sink dynamics. *Ecol Evol*. <https://doi.org/10.1002/ece3.2029>
- Heinrichs JA, Lawler JJ, Schumaker NH, Wilsely CB, Monroe KC, Aldridge CL (2018) A multispecies test of source-sink indicators to prioritize habitat for declining populations. *Conserv Biol* 32:648–657
- Holt RD (1985) Population dynamics in two-patch environments: some anomalous consequences of an optimal habitat distribution. *Theor Popul Biol* 28:181–208
- Kanda LL, Fuller TK, Sievert PR, Kellogg RL (2009) Seasonal source-sink dynamics at the edge of a species' range. *Ecology* 90:1574–1585
- Kostecke RM, Cimprich DA (2008) Adult and Juvenile survival of black-capped vireos within a large breeding population in Texas. *The Condor* 110:251–259
- Loreau M, Daufresne T, Gonzalez A, Gravel D, Guichard F, Leroux SJ, Loeuille N, Massol F, Mouquet N (2013) Unifying sources and sinks in ecology and earth sciences. *Biol Rev Camb Philos Soc* 88:365–379
- Morris DW (2011) Source–sink dynamics emerging from unstable ideal freehabitat selection. In: Liu J, Hull V, Morzillo AT, Wiens JA (eds) Sources, sinks and sustainability. Cambridge University Press, Cambridge, pp 58–81
- Pulliam RH (1988) Sources, sinks, and population regulation. *Am Nat* 132:652–661
- Ratzliff A (1987) Endangered and threatened wildlife and plants: determination of the black-capped vireo to be an endangered species. *Fed Reg* 52:37420–37423
- Runge JP, Runge MC, Nichols JD (2006) The role of local populations within a landscape context: defining and classifying sources and sinks. *Am Nat* 167:925–938
- Schumaker NH, Brookes A (2018) HexSim: a modeling environment for ecology and conservation. *Landscape Ecol*. <https://doi.org/10.1007/s10980-017-0605-9>
- U.S. Geological Survey, 20140331, NLCD 2011 Land Cover (2011) U.S. Geological Survey, Sioux Falls, SD
- Vega Rivera JH, Ortega-Huerta MA, Sarkar S, Rappole JH (2011) Modelling the potential winter distribution of the endangered Black-capped Vireo (*Vireo atricapilla*). *Bird Conserv Int* 21:92–106
- Walker L (2015) Population dynamics of the endangered Black-capped Vireo (*Vireo atricapilla*)
- Walker LE, Marzluff JM, Cimprich DA (2016) Source-sink population dynamics driven by a brood parasite: a case study of an endangered songbird, the black-capped vireo. *Biol Conserv* 203:108–118
- Weegman MD, Bearhop S, Fox AD, Hilton GM, Walsh AJ, McDonald JL, Hodgson DJ (2016) Integrated population modelling reveals a perceived source to be a cryptic sink. *J Anim Ecol* 85:467–475
- Wilkins N, Powell RA, Conkey AAT, Snelgrove AG (2006) Population status and threat analysis for the black-capped vireo. Department of Wildlife and Fisheries Sciences, Texas A&M University, College Station, TX
- Wilsey CB, Lawler JJ, Cimprich DA (2012) Performance of habitat suitability models for the endangered black-capped vireo built with remotely-sensed data. *Remote Sens Environ* 119:35–42
- Wilsey CB, Lawler JJ, Cimprich D, Schumaker NH (2014) Dependence of the endangered black-capped vireo on sustained cowbird management. *Conserv Biol* 28:561–571