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Contributed Papers

Divergence in sink contributions to population persistence

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Abstract: *Population sinks present unique conservation challenges. The loss of individuals in sinks can compromise persistence; but conversely, sinks can improve viability by improving connectivity and facilitating the recolonization of vacant sources. To assess the contribution of sinks to regional population persistence of declining populations, we simulated source–sink dynamics for 3 very different endangered species: Black-capped Vireos* (Vireo atricapilla) *at Fort Hood, Texas, Ord's kangaroo rats* (Dipodomys ordii) *in Alberta, and Northern Spotted Owls* (Strix occidentalis caurina) *in the northwestern United States. We used empirical data from these case studies to parameterize spatially explicit individual-based models. We then used the models to quantify population abundance and persistence with and without long-term sinks. The contributions of sink habitats varied widely. Sinks were detrimental, particularly when they functioned as strong sinks with few emigrants in declining populations (e.g., Alberta's Ord's kangaroo rat) and benign in robust populations (e.g., Black-capped Vireos) when Brown-headed Cowbird* (Molothrus ater) *parasitism was controlled. Sinks, including ecological traps, were also crucial in delaying declines when there were few sources (e.g., in Black-capped Vireo populations with no Cowbird control). Sink contributions were also nuanced. For example, sinks that supported large, variable populations were subject to greater extinction risk (e.g., Northern Spotted Owls). In each of our case studies, new context-dependent sinks emerged, underscoring the dynamic nature of sources and sinks and the need for frequent re-assessment. Our results imply that management actions based on assumptions that sink habitats are generally harmful or helpful risk undermining conservation efforts for declining populations.*

Keywords: *Dipodomys ordii*, ecological traps, population persistence, sink contributions, source–sink dynamics, spatially explicit individual-based model, *Strix occidentalis caurina*, *Vireo atricapilla*

Divergencia en las Contribuciones de Vertedero a la Persistencia Poblacional

Resumen: *Los vertederos poblacionales son retos de conservación únicos. La pérdida de individuos en los vertederos puede comprometer la persistencia, pero en contraste, los vertederos pueden aumentar la viabilidad al mejorar la conectividad y al facilitar la recolonización de las fuentes vacantes. Para evaluar la contribución de los vertederos a la persistencia poblacional de las poblaciones declinantes simulamos las dinámicas de fuente-vertedero de tres especies en peligro muy diferentes: el víreo de cabeza negra* (Vireo atricapilla) *en Fort Hood, Texas; la rata canguro de Ord* (Dipodomys ordii) *en Alberta; y el búho moteado del norte* (Strix occidentalis caurina) *en el noroeste de los Estados Unidos. Usamos datos empíricos de estos estudios de caso para hacer parámetros para los modelos espacialmente explícitos basados en individuos. Después utilizamos los modelos para cuantificar la abundancia y la persistencia poblacional con y sin los vertederos a largo plazo. Las contribuciones de los hábitats vertedero variaron ampliamente. Los vertederos fueron dañinos, particularmente cuando funcionaron como vertederos de hoyo negro, para las poblaciones declinantes (p. ej.: la rata canguro) y benignos para las poblaciones robustas (p. ej.: los víreos) cuando se controló el parasitismo del tordo de cabeza café* (Molothrus ater). *Las contribuciones de vertedero también estuvieron matizadas.*

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Por ejemplo, los vertederos que mantuvieron poblaciones grandes y variables estuvieron sujetos a mayores riesgos de extinción (p. ej.: los búhos moteados). En cada uno de nuestros estudios de caso surgieron vertederos nuevos dependientes del contexto, lo que enfatiza la naturaleza dinámica de nuestras fuentes y vertederos y la necesidad de una reevaluación frecuente. Nuestros resultados implican que las acciones de manejo con base en la suposición de que los hábitats vertedero son generalmente dañinos o útiles corren el riesgo de debilitar los esfuerzos de conservación para las poblaciones declinantes.

Palabras Clave: contribuciones de vertedero, dinámicas de fuente-vertedero, modelo espacialmente explícito basado en individuos, persistencia poblacional, trampas ecológicas, *Dipodomys ordii*, *Strix occidentalis caurina*, *Vireo atricapilla*

Introduction

A growing body of modeling and empirical studies suggest that population sources and sinks may be common in nature (Wiens & Van Horne 2011) and increasingly prevalent in rapidly changing landscapes. A large number of individuals may occupy sink habitats (where births < deaths and emigration < immigration), particularly in human-modified landscapes, making the appropriate management of sinks (Pulliam 1988) a key element in long-term conservation planning for species at risk of decline and extinction (Howe et al. 1991). Yet much of the source–sink theory and literature pertains to stable equilibrium populations in static environments. Hence, the degree to which predictions based on classical source–sink biology apply to declining and imperiled species remains unclear.

Source–sink theory has also largely developed from mathematical approaches, creating hypotheses that are often difficult to test with empirical data. Thus, managing declining populations and populations in variable environments based on conclusions drawn from equilibrium population theories may prove ineffective. Using an innovative spatially explicit agent-based modeling approach, we explored the emergence and severity of source–sink dynamics in a range of populations at risk of decline and extinction. We used a series of case studies to explore the nuances of how source–sink dynamics operate in nonequilibrium empirical systems. Drawing from the source–sink literature, we assessed the factors and circumstances under which sinks are expected to improve or reduce population size and persistence. We simulated the removal of sinks to assess their contributions to population size and persistence in each case and devised hypotheses for further evaluation.

The impact of sink habitats on regional population persistence is likely to depend on a number of factors, including the nature of the species, the spatial patterns of sources and sinks, and population size and trajectory. In declining populations with low growth rates, persistence may depend more on the impacts of sinks than sources (habitats in which births > deaths and emigration > immigration; Pulliam 1988; Howe et al. 1991). With few individuals and small margins for loss in sink habitats, small declining populations may be more sensitive to the presence of sink habitats than large stable populations. Conversely, small populations may also benefit more from the short-term benefits of sinks than larger populations. For example, sinks can bolster regional abundance, which helps avert stochastic extinction of small populations.

Highly Dynamic Populations

In changing environments, sinks (in addition to sources) can function in the short term as refuges from spatially asynchronous perturbations, harboring individuals that can emigrate or produce offspring that later disperse to sites of local extinctions (e.g., Foppen et al. 2000; Frouz & Kindlmann 2001; Falcy & Danielson 2011). In highly variable environments, weaker sinks can also temporarily behave like sources during periods of favorable conditions and contribute to population growth. Pseudosinks (i.e., sources that behave like sinks when densities are high) can revert to source conditions under low densities (Watkinson & Sutherland 1995; Dias 1996; Johnson 2004). Even relatively consistent sinks may prove beneficial in the long term if the ecological context or landscape undergoes substantial directional change.

Strong Sinks and Ecological Traps

Suboptimal sites such as sinks generally do not provide long-term habitat (Van Horne 1983; Howe et al. 1991) and the presence of sink habitats within a regional network may be ultimately detrimental to population persistence. The degree to which sinks compromise persistence may depend on their strength. The presence of strong sinks, with a large ratio of deaths to births, may reduce regional population size and persistence. Gunderson et al. (2001) found that high mortality rates in sinks could lead to reduced population growth in sources. Similarly, Delibes et al. (2001*b*) concluded that sufficiently high mortality in sinks could lead to extinction of subpopulations in sources. The impact of strong sinks may be magnified in areas where few individuals are able to survive and emigrate elsewhere (Holt & Gaines 1992). Similarly, ecological traps (low-quality habitats that are preferred over high-quality habitats) may be particularly detrimental if they attract and divert a substantial number of immigrants away from source habitats (Howe et al. 1991; Battin 2004).

Sinks That Facilitate Connectivity

The presence of sinks in a fragmented or disconnected system may aid in connecting source populations, which strengthens abundance and persistence. Sinks may provide corridors (e.g., linear features such as roads, cutlines) or stepping stones (e.g., discrete patches) that facilitate dispersal and allow individuals to avoid saturated habitats and more widely distribute themselves among source populations (Vögeli et al. 2010).

To assess the roles of sink habitats and determine the consistency with which they affect the persistence of species of conservation concern, we used empirical data to simulate source–sink dynamics for three very different endangered species. We quantified population abundance and persistence, with and without long-term sinks, and assessed the degree to which sinks affect long-term population outcomes. We considered the implications of our findings for prioritizing source and sink habitats for management and the potential consequences of misdiagnosing sink contributions in each case study. Using our case-study results, we developed sink contribution hypotheses for strong sinks and ecological traps, sinks in highly dynamic populations, and sinks that facilitate connectivity.

Methods

Case Studies

We simulated source–sink dynamics for three endangered species: Black-capped Vireos (*Vireo atricapilla*) at Fort Hood, Texas (U.S.A.), Ord's kangaroo rats (*Dipodomys ordii*) in Alberta, Canada, and Northern Spotted Owls (*Strix occidentalis caurina*) in the northwestern United States. We chose these species in part because they represent small and declining populations in a range of ecological contexts in which sink contributions to population persistence may differ. They occupy very different landscapes with different sink strengths and magnitudes of population fluctuations; have a range of population sizes, trends, and rates of decline; and are subject to different drivers of source–sink dynamics (habitat quality, nest parasitism, interspecific competition, etc.). More specifically, the Black-capped Vireo and Northern Spotted Owl systems are thought to contain ecological traps or strong sinks, and Canada's Ord's kangaroo rats are an example of a highly dynamic population with sinks that facilitate connectivity. We used empirical data to construct spatially explicit, individual-based models in the HexSim simulation modeling environment (Schumaker 2013). HexSim is designed for simulating terrestrial wildlife population dynamics and interactions. The software provides a flexible modeling framework in which users define the model structure and supply spatial data, demographic data, and behavioral parameters to create unique models for different populations or species. This approach allows sources and sinks to be emergent properties of the simulations.

Ecological Traps and Potentially Rapid Decline of Vireos

On the Fort Hood military installation, the Black-capped Vireo occupies relatively discrete shrubby habitat patches in a landscape shared with Brown-headed Cowbirds (*Molothrus ater*). Brown-headed Cowbirds have expanded their range and parasitize Vireo nests in previously high-quality Vireo habitat; thus, Cowbirds have functionally converted these areas into ecological traps that may limit population persistence (Gates & Germaine 1978; Remes 2000; Battin 2004). Hence, the source-trap status of Vireo habitat is largely driven by parasitism pressure and the presence or absence of Cowbird control. The population has been deemed conservation reliant and requires the ongoing removal of Cowbirds to maintain population stability (Wilsey et al. 2014) and avoid potentially rapid decline. Using the population model developed by Wilsey et al. (2014), we simulated realistic scenarios of Vireo source–sink dynamics in the presence and absence of Cowbird control and assessed the role of sinks in both cases. In the absence of Cowbird control, Vireos were affected by high parasitism rates (75% in high- and 85% in low-quality habitat [Wilkins et al. 2006]). Under Cowbird control, Vireos were subject to low parasitism rates (5% in high- and 15% in low-quality habitat).

Highly Dynamic Populations of Kangaroo Rats with Connective Sinks

Canada's Ord's kangaroo rat occupies discrete sandy habitat patches in southern Alberta, including actively eroding sand dunes or blowouts, semi-stabilized sand dunes, and the margins of sandy roads (Gummer et al. 1997; Gummer 1999; COSEWIC 2006). Sinks arise from differences in habitat quality among habitat types. Sandy roads and associated disturbed ground are known to facilitate movement but are associated with higher rates of disturbance, predation, parasitism, low forage quality, cold burrows, and low overwinter survival rates (Teucher 2007). This highly dynamic population experiences substantial seasonal and inter-annual fluctuations in abundance (COSEWIC 2006). High seasonal reproductive rates can lead to opportunistic occupancy of low-quality habitats, where overwinter survival can be < 10%, and extirpation in patches is common (Kenny 1989; Gummer et al. 1997; Gummer & Robertson 2003). Heinrichs et al. (2010)

found that sinks tended to have negative impacts on the kangaroo rat population. We expanded this simulation to quantify the effects of sink removal on population size, variability, patch occupancy, and source–sink dynamics.

Strong Sinks in Northern Spotted Owl Populations

The range of the Northern Spotted Owl spans several states along the pacific coast, where there is continuous variation in habitat quality rather than discrete, local habitat patches. Principal threats to the Spotted Owl include habitat loss and degradation, loss of habitat connectivity, and increasing competition with an invasive species (i.e., Barred Owls [*Strix varia*] [USFWS 1992]). Interspecific competition with Barred Owls presents an important range-wide threat. In a shrinking landscape, owl species compete for breeding and foraging habitat, and the increasing number of Barred Owls has reduced Spotted Owl site occupancy, reproduction, and survival rates (USFWS 2011). Sources and sinks primarily result from differential habitat quality and interspecific interactions with Barred Owls. Our Northern Spotted Owl model (adapted from Schumaker et al. [2014]) simulated region-specific encounter rates with Barred Owls. Habitat-quality-dependent Spotted Owl survival rates were lower in the presence of Barred Owls, resulting in different sink strengths (including some strong sinks). The model was parameterized with data from several smaller spatial demographic modeling regions in the northwestern United States.

Simulations

Habitat maps for each species were derived from empirical habitat suitability models and linked with empirically derived demography or density, range size, and movement data within the spatially explicit individual-based models. Modeled individuals dispersed among patches or areas of the landscape to select a suitable range. The amount and quality of resources within each range influenced simulated density, and individual survival and reproduction rates. Habitat-specific survival rates were used to describe differences in habitat quality for kangaroo rats, and habitat suitability values were assumed to represent habitat quality for Vireos and Spotted Owls. All models included environmental stochasticity (Supporting Information).

Behaviors of animals in sources and sinks were emergent properties of our simulations and resulted from collective experiences of individuals in each patch. The source–sink status of a patch was influenced by the constraints and opportunities provided by the habitat (e.g., patch quality, location, size, shape) and the species and population attributes (life history characteristics including demographic structure and rates, population size, etc.), interspecific interactions (e.g., parasitism by Cowbirds, competition with Barred Owls), and movement. For each patch or sampling block, the total number of births minus deaths was recorded (hereafter referred to as productivity) and provided the basis for classifying sources and sinks. Patches in which the number of deaths exceeded births over 100 years (i.e., negative productivity values) were deemed long-term sink habitats (and vice versa for sources; positive productivity values). The strength of sinks was characterized by the degree to which productivity values differed from zero. Sinks were deemed weak if productivity values were close to zero (i.e., –200 to 0) and strong if values were far from neutral (i.e., –201 to –35,000). Immigration and emigration movements were implicitly represented in source–sink calculations; dispersal events influenced source–sink status by altering the number of subsequent births and deaths in the new location (Supporting Information). For each species and scenario, we conducted 100 stochastic model runs. The details of each model are in Wilsey et al. (2014), Heinrichs et al. (2010), and Schumaker et al. (2014), and are summarized in Supporting Information.

For each species, initial (baseline) model runs were conducted to identify long-term (100 years) sink habitats. Sink habitat patches were then digitally removed from the habitat map and replaced with nonhabitat matrix. Because owl habitat was difficult to discretize, we used 34 sampling blocks (8,417 km^2) rather than patches or larger management zones to identify source and sink regions. Simulations were re-run with landscapes composed only of areas identified as long-term sources in the baseline runs. For all simulations, population size, variability, and trajectory were recorded, along with patch occupancy and regional population extinction-risk measures. To assess the impact of sinks on the populations of the 3 species, we directly compared metrics derived from the baseline (including sinks) and sink-removal scenarios.

Results

Black-Capped Vireo

Under the active Cowbird control scenario, there was little risk of regional population extinction (Fig. 1a). Low rates of nest parasitism produced a stable Vireo population of 4,500–5,000 breeding pairs occupying 97% of habitat patches. Sources generally coincided with areas of high-quality habitat. Approximately half the patches were classified as long-term sinks, 64% of all habitats (Table 1). Sinks were generally small and peripheral to source patches (Supporting Information). The removal of all sinks had no observable effect on population size or variability, trajectory, or extinction risk (Fig. 1a). The number and strength of sources differed little among baseline and sink-removal scenarios. A few new, weaker

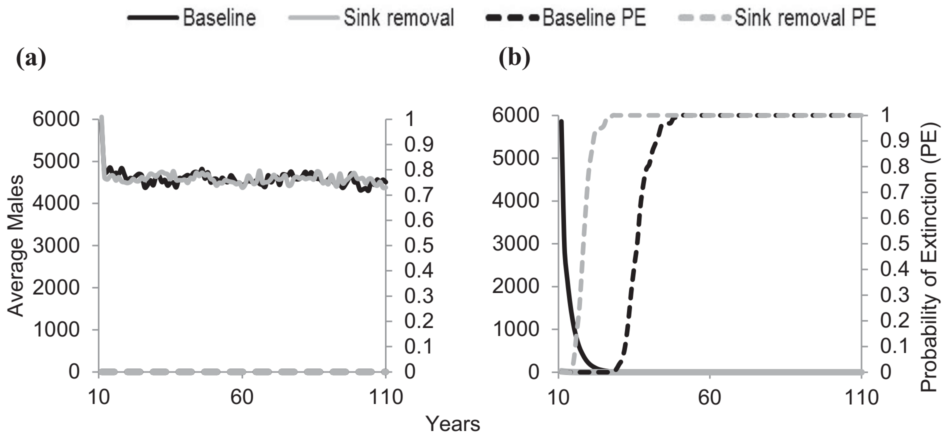

Figure 1. Black-capped Vireo population size and extinction risk under (a) Cowbird control and (b) no Cowbird control in baseline (i.e., including all habitat and sink habitat removal scenarios over time). The population size in the sink removal scenario is very small (appearing as nearly 0) and declines to 0 at approximately year 30.

Table 1. Summary of species-specific productivity data for baseline (base) and removal of habitat sinks (rem) scenarios.

	Black-capped Vireo							
	Cowbird control		*no Cowbird control*		*Ord's kangaroo rat*		*Northern Spotted Owl*	
Habitat characteristic	*base*	*rem*	*base*	*rem*	*base*	*rem*	*base*	*rem*
Habitat patches								
total	2,975	1,478	2,975	1,347	6,414	5,178	34	8
occupied (%)	97	97	59	7	26	7	100	100
(*n*)	(2,896)	(1,435)	(1,742)	(93)	(1,655)	(365)	(34)	(8)
habitat removed[a] (%)		64		98		17		78
Sink habitats								
number	1,497	36	1,628	55	1,236	159	26	6
mean productivity max	−7	−2	−196	−2	−19	−6	−4,974	−6,886
productivity	−59	−5	−33,350	−3	−1,376	−42	−12,454	−12,956
productivity SD	4	1	1,509	1	61	7	3,687	5,526
Source habitats								
number	1,399	1,399	81	20	342	185	8	2
mean productivity max	3,987	3,992	1,862	1	363	644	6,215	2,285
productivity	7,35,706	7,38,694	2,934	2	45,527	43,828	22,848	4,509
productivity SD	34,799	34,882	943	1	2,728	3,586	7,214	3,146

[a] *Sink habitat patches were digitally removed from the habitat map and replaced with nonhabitat matrix.*

sinks (36) emerged from previously unoccupied patches, all of which were relatively small and peripherally located (Supporting Information).

In the absence of Cowbird control measures, Vireos rapidly declined toward extinction (Fig. 1b). Under high parasitism pressure, the removal of all sinks (and 98% of habitat) accelerated population decline. Time to extinction was reduced from approximately 40 years to 20 years. The remaining sources (20) were weak, with a nearly equal number of births and deaths. New sinks (55) emerged from previously unoccupied, neutral, or source patches. All were relatively small, and most were located on the periphery of larger patch complexes.

In the absence of Cowbird control, patch occupancy was low (59%) and the remaining sources (81) were weaker than those in the Cowbird control scenario. The strongest of these weak sources had <0.3% of the productivity of that in the Cowbird control scenarios, and average source productivity was half that of sources in the Cowbird control scenario (Table 1). Most (93%) of the occupied patches were population sinks. On average, sinks in the absence of Cowbird control were 28 times stronger than those with Cowbird control. In the absence of Cowbird control, the least productive sink was >500 times the strength of the strongest sink under Cowbird control.

Ord's Kangaroo Rat

In the presence of sinks in the baseline simulation, the kangaroo rat population declined to a small size and exhibited a corresponding increase in extinction risk (Fig. 2). A small percentage of patches were occupied (approximately 26%; Table 1), which left vacant many of the small, isolated (but otherwise suitable) patches in the landscape. Active sand dunes functioned as long-term population sources, as did a smaller proportion of

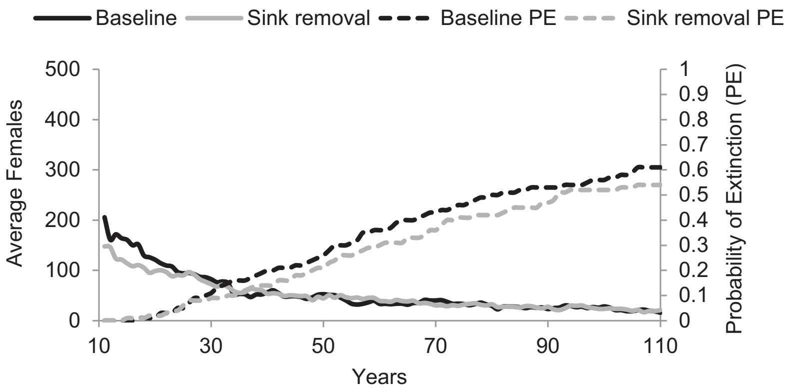

Figure 2. Change in kangaroo rat population size and extinction risk in baseline (i.e., with all habitat) and sink-removal scenarios over time.

other patch types. The remainder of occupied patches functioned as long-term population sinks, including many road segments, semi-stabilized sand dunes, and exposed soil areas (Supporting Information).

When all sinks identified in the baseline scenario (1,236) were removed, the probability of extinction was reduced by about 0.1 (Fig. 2). Despite a 17% reduction in the amount of habitat, there was little change in mean population size. The average strength of remaining sources increased, but almost half the original source patches (46%) transitioned to another state (i.e., became unoccupied, neutral, or sinks). Newly emerging sinks (159) were (on average) three times weaker than those in the baseline scenario. The new sinks were often adjacent to areas of high productivity (i.e., sources) (Supporting Information), which suggests that some may be pseudosinks.

Northern Spotted Owl

When projected 100 years into the future, the Spotted Owl population declined, and extinction risk increased correspondingly through time. All habitat was occupied in the baseline scenario, and the majority of areas (26 of 34 total sampling blocks) acted as population sinks (Supporting Information). Removal of observed demographic sinks (which were caused in part by Barred Owls) eliminated roughly 78% of available habitat, thus causing a dramatic reduction in population size (Fig. 3) and variability (results not shown). The smaller, more stable regional population exhibited a lower risk of extinction. When sinks were removed, 2 of the 8 original sources remained as connected sources but had reduced productivity (and reduced variability in productivity). Six areas that were sources in the baseline simulation became sinks. These new sinks were stronger and more variable than the original sinks that were removed, and owl density increased, except in one area, indicating that these may be pseudosinks. In general, the amount of sink habitat removed did not predict sink contributions.

Discussion

The loss of many organisms in sink habitats may lead to the conclusion that sinks are often harmful for long-term persistence (Hansen 2011; Wiens & Van Horne 2011). However, surviving sink occupants can bolster regional population sizes, increase a population's distribution, and occasionally rescue source populations (Holt 1985; Pulliam 1988; Falcy & Danielson 2011), possibly encouraging the opposite generalization (i.e., that sinks are helpful for long-term population persistence). Despite theoretical progress, little is known about how sinks function in complex empirical systems and contribute to the persistence of small, declining populations. We simulated the removal of sinks to assess the degree to which sinks actually support or compromise abundance and persistence in each case study. Our results demonstrate that sinks can be both harmful and helpful depending on the ecological context (Table 2) and suggest that the impact of sinks can be difficult to infer from the strength of sinks, the amount of variability in the system, and the degree to which sinks facilitate movement. Management actions based on untested generalizations of sink contributions could result in adverse consequences for many species of conservation concern.

Strong Sinks and Ecological Traps

Strong sinks are often thought to absorb individuals that could have otherwise occupied source habitat, which reduces source occupancy and abundance. Similarly, ecological traps are generally characterized as detrimental to populations (e.g., Delibes et al. 2001*a*; Kristan 2003; Battin 2004). However, strong sinks and ecological traps are not universally detrimental to regional populations. Our results suggest that the impact of traps on long-term population persistence can depend on whether the population is stable or declining and on the availability of source habitat (e.g., Black-capped Vireos). The impact of strong sinks also depends on the degree to which sinks bolster abundance and stabilize population dynamics (e.g., Northern Spotted Owls).

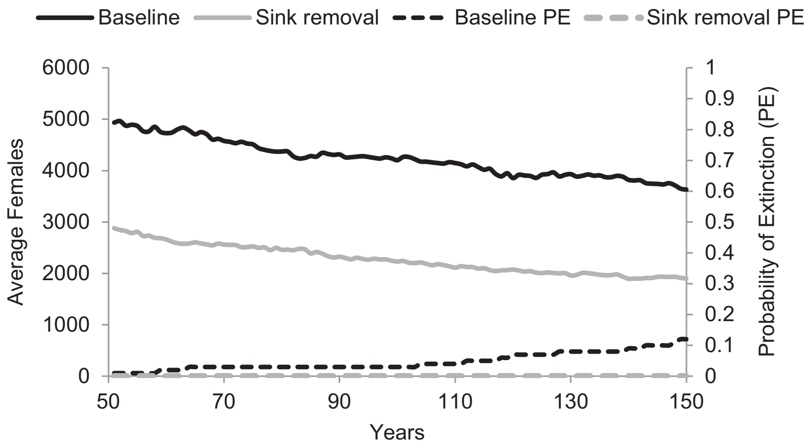

Figure 3. Change in Northern Spotted Owl population size and extinction risk baseline (i.e., with all habitat) and sink-removal scenarios over time.

Table 2. Expected and observed contributions of sinks to population size and persistence, with positive, negative, and neutral effects when sinks are removed.

Sink type	*Possible sink contribution*	*Observed sink contribution*	*Case study*
Strong sinks and ecological traps	occupancy of or attraction to sinks diverts individuals away from sources, reducing population sizes in sources (negative)	stable population with high source occupancy (neutral) rapidly declining population with few sources (negative) sink destabilize dynamics (negative) sinks bolster population size (positive)	Black-capped Vireo—Brown-headed Cowbird control Black-capped Vireo—no Cowbird control Northern Spotted Owl
Sinks in highly dynamic populations	sinks bolster population sizes (positive) sinks rescue sources during population fluctuations (positive)	sinks emit few individuals back to sources in unfavorable years (negative)	Ord's kangaroo rat
Sinks facilitating connectivity	increase distribution, occupancy, and recolonization of sources (positive)	intervening sinks direct movement away from sources and lower occupancy of sources (negative)	Ord's kangaroo rat

Under our Cowbird control scenario (low parasitism pressure), Vireos increased to a stable regional population size with well occupied, highly productive sources. Population size, extinction risk, and occupancy rates differed little among baseline and removal scenarios, and ecological traps, which constituted the majority of habitat by area, contributed little to overall Vireo population dynamics and persistence. A single change in ecological context in the Vireo system (removing Cowbird control) yielded very different results. Under high parasitism pressure, the population rapidly declined toward extinction. Although the same amount of habitat was available in both baseline scenarios, traps were stronger and fewer birds were able to persist without Cowbird control, resulting in lower occupancy and source productivity values, and nearly all Vireo patches and populations were classified as traps. With few sources, the regional population became dependent on traps to delay extinction. This yielded a positive, albeit short-term, contribution to persistence. Although trap habitats do not always support long-term persistence, their continued presence in landscapes with little and sub-optimal habitat may provide a window of opportunity during which management actions could address and reverse the causes of decline for populations at risk of near-term extinction.

The influence of strong population sinks on population outcomes can also depend on the degree to which sinks increase abundance and stabilize population dynamics. In the Spotted Owl system, sinks had different and sometimes contradictory influences on population size, stability, and extinction risk. The removal of sinks, along with a large proportion of habitat (78%), caused a reduction in population size of approximately 40% (about 2000 females), but it also lowered the risk of extinction. Smaller populations are generally thought to be more vulnerable to extinction as a result of stochastic events; however, in this case, the smaller post-removal population sizes were less variable than those in the pre-removal landscape under similar stochastic conditions.

Highly Dynamic Populations

Sinks in spatially and temporally fluctuating systems have the potential to make a positive contribution to persistence. Although sinks can be beneficial, they are unlikely to be crucial for all declining populations in variable environments. Among other factors, the contributions of sinks to regional persistence are likely to depend on the characteristics of the sinks and the nature of the population variation. In kangaroo rats, high seasonal reproduction and emigration from sources can result in pulsed occupancy of sink habitats. In favorable years, sinks can bolster regional population sizes and provide emigrants to rescue sources after local stochastic extinctions. However, in unfavorable years, few kangaroo rats survive the winter in strong sinks, which limits contributions to overall population size and has a net negative influence on long-term persistence. Sink contributions may be positive in systems where the favorable years outnumber the unfavorable, where environmental perturbations are spatially asynchronous, and in systems with a high degree of sink emigration to sources. Future changes in habitat (e.g., affecting sources but not sinks) and interspecific conditions (e.g., spatially varying parasitism, competition) may prompt current Vireo and Spotted Owl dynamics to become much more variable. This may cause some detrimental sinks to become beneficial under changing conditions.

Sinks That Facilitate Connectivity

In favorable conditions, sinks are thought to serve as stepping stones (i.e., connecting sources) that increase distribution, re-colonization success, and source occupancy. However, our results suggest that a net positive contribution of connective sinks is likely to depend on the configuration of sources and sinks, the species' ability to discriminate among low- and high-quality habitats, and their success in emigrating to sources. In the kangaroo rat system, the margins of sandy roads facilitate movement throughout the landscape, but the observed inability of kangaroo rats to discriminate among low and high-quality sites led to the opportunistic occupancy of easily found road margins over sand dunes, which left high-quality areas under-saturated. Harsh overwinter conditions often restricted the life span of kangaroo rats to <1 year in poor-quality areas, limiting emigration from low-quality habitats and weakening the ability of individuals in sinks to emigrate to sources in future years. In the Northern Spotted Owl landscape, sinks that connected source populations facilitated movement among high-quality areas to a greater extent than when replaced with matrix, but they did not improve persistence. Sinks that facilitate connectivity may be more important for Vireos during migration (i.e., at a broader spatial extent) than in breeding habitat. Connecting sinks may be more beneficial in systems where source areas are easily found and preferred over sinks and where sink conditions permit successful emigration to sources.

Dynamic Nature of Sources and Sinks

Sources and sinks are emergent properties of the interaction of a host of population and habitat variables (Dunning et al. 1992; Loreau et al. 2013). Sink contributions are likely to be further influenced by the key factors driving source–sink dynamics, including species characteristics, population size, rate of growth or decline, landscape attributes, ratio of sources to sinks, and the amount and connectivity of habitat. Hence, it is not surprising that even with our simplistic approach of simulating the removal of all sink habitat, new context-dependent sinks emerged with changes in occupancy, density, and distributions. Despite the wide range of sink contributions, the emergence of novel (context-dependent) sinks was consistent among cases in post-removal landscapes. This result underscores the fact that sources-sink status is a largely context-dependent label, requiring re-evaluation with concurrent environmental and ecological shifts.

Populations at risk of decline and extinction are often affected by multiple factors that influence and modify sink contributions to persistence, and accurately assessing the contributions of sinks to population dynamics and persistence can be challenging, particularly in systems with complex source–sink dynamics. Repeated and multi-scale assessments of the factors influencing local and regional source–sink dynamics are likely required to estimate the short- and long-term influences of sink habitats on population persistence and to effectively inform the conservation and management of sink habitats and populations. Because our aim was to assess the consistency of sink contributions to population persistence from a very general perspective, our results describe long-term, average contributions. However, for management aims, future research should examine the sensitivity of source–sink classifications and associated sink contributions to the metrics and the periods used to define them. In particular, the success of Northern Spotted Owl management actions is likely to depend on robust characterizations of sinks and their impacts on persistence. In largely contiguous or space-filling landscapes, multiple spatial scales should be assessed to identify the most appropriate scale of analysis (Supporting Information) (Loreau et al. 2013; Schumaker et al. 2014).

Conservation and Management of Sinks

Source populations are, appropriately, the focus of conservation and management efforts because they often provide the stable populations required for long-term regional persistence (Dias 1996). Yet sinks can make important contributions to conservation goals. Under some circumstances, conservation actions aimed at sinks can be more effective than those aimed at sources. For example, in landscapes with recurring disturbance in sources (but not sinks), improvements in growth rates in sinks can be more effective than increasing the rate of post-disturbance habitat recovery (Falcy & Danielson 2011; Wiens & Van Horne 2011). In conservation-reliant species, the strength and impact of sinks and traps can be directly linked to management actions (e.g., Brown-headed Cowbird control for Black-capped Vireos). Increasing Cowbird control can increase reproductive success, weaken ecological traps, and is likely to be more effective than source habitat improvements. In general, an understanding of how the intensity of Cowbird control influences the strength of traps and their resulting contributions to persistence may inform selection of target areas (e.g., to maintain existing source areas) and intensity of control in nonsource areas. Active management of sink populations may also be a viable addition or alternative when conservation actions aimed at sources are limited by the practical constraints of land ownership and cost.

Our results support the idea that sinks can be helpful in improving long-term persistence, but we caution against conservation and management actions based on generalizations of sink contributions. Although sinks can facilitate connectivity and bolster population sizes in dynamic systems, sinks are not always beneficial in the long term. Sink contributions may be detrimental in rapidly declining populations and in landscapes with few sources and problematic if sinks keep or divert emigrants away from sources. For example, despite the potential for sinks to make positive contributions to kangaroo rat persistence (by increasing population size and distribution), the continued proliferation of low-quality areas (including roads) is likely to be detrimental if kangaroo rats continue to occupy poor areas over high-quality sand dunes. Accurately identifying sinks and removing them (e.g., restoring sink roads and their margins) could improve persistence.

Source–sink status and strength should be expected to vary through time, with environmental variability and directional system changes. In systems with greater dependence on sink populations, management actions based on frequent and accurate assessments of sink habitats could mean the difference between the preservation and loss of species. For species at risk of decline and extinction, frequent monitoring of sink habitats (in addition to source habitats) might also identify opportunities for long-term or temporary improvements (e.g., partial habitat restoration, temporary competitor or parasite control, or supplemental feeding during times of scarcity) that enhance the contribution of sinks to persistence. In systems with greater dependence on source populations, frequent assessments of sink contributions can also aid in prioritizing sink habitats for conservation, recovery, or removal as population dynamics respond to variable and shifting conditions.

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Supporting Information

Additional model information (Appendix S1) and sink removal maps (Appendix S2) are available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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