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Recent Advances and Current Challenges in Applying Source-Sink Theory to Species Conservation

Julie A. Heinrichs [1,2] · Lauren E. Walker [1,3] · Joshua J. Lawler [1] · Nathan H. Schumaker [4] · Kira C. Monroe [1,2] · Amy D. Bleisch [1]

Abstract

Purpose of Review The source-sink paradigm has been a powerful tool for focusing theoretical and empirical explorations of population dynamics in heterogeneous landscapes. The prevalence of suspected source-sink dynamics in empirical studies would lead to the conclusion that sources and sinks are common. However, important questions remain about how source-sink dynamics have been assessed in past studies and the degree to which current approaches apply to atypical populations and dynamic landscapes.

Recent Findings We reviewed 432 papers that directly addressed source-sink dynamics between 1985 and 2018. We found that the majority of studies focused on birds, mammals, and forested systems. In recent years, however, the number of aquatic invertebrate and marine studies increased, as did the tendency to focus on conservation or management goals and to report population trends. Although 79% of papers claimed to identify source-sink dynamics, only 13% of studies based their assessment on all four measures of reproduction, mortality, immigration, and emigration. Nearly 23% of all studies used neither demographic nor movement metrics to make conclusions about the presence of source-sink dynamics.

Summary Source-sink theory and practice has matured and is increasingly relevant for species conservation and management. However, we lack a clear understanding of the conditions under which limited data can defensibly support source-sink assessments and be scaled up to the extent at which resource decisions are made. In the absence of this, future studies will need to take a more rigorous approach to defining sources and sinks to better gauge the prevalence of source-sink dynamics.

Keywords Source-sink dynamics · Source · Sink · Review · Conservation · Metapopulation

Introduction

Source-sink dynamics emerged as an important ecological concept in the 1980s [1, 2] and grew in influence through subsequent decades [3]. Source-sink theory and ideas now influence how ecologists study spatially structured populations, and source-sink assessments are increasingly considered in conservation and management decisions. The concept describes population performance as influenced by reproduction, mortality, and movements in and out of local populations that are separated by matrix or less suitable habitat in a regional population network. Sources are self-sufficient net exporters of organisms, with a greater number of births than deaths. In sinks, deaths outnumber births [1] and immigration becomes necessary to support the local population [4].

Differences in local demography and movement within a regional population network can emerge from variation in habitat quality and population conditions within patches; hence, source-sink dynamics are often driven by spatial heterogeneity [5]. This heterogeneity can result from natural processes or from anthropogenic environmental changes [6–8], prompting practitioners to assess sources and sinks in a range of empirical systems. Source-sink dynamics can be

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strengthened (i.e., experience an increase in the disparity among sources and sinks) in landscapes with disparate patch sizes and qualities, and where sources and sinks are interspersed [9]. In addition, the presence and strength of source-sink dynamics can be influenced by species' life history traits and overall population trends [9, 10].

Source-Sink Metrics

Since the conceptualization of source-sink dynamics, a number of different approaches and metrics have been used to identify sources and sinks. Founding source-sink papers relied primarily on the difference between birth and death as well as immigration and emigration (BIDE) counts or rates to characterize local source and sink properties [1]. Other researchers have used simple population metrics such as local abundance and density to indicate source or sink status [e.g., 11]. Yet, simplified metrics are generally inconsistent predictors of source-sink status [3] as presence, density, and abundance can be poorly correlated with local habitat quality and population productivity, particularly in sinks [8, 12]. Papers that have used both demography and movement to assess source-sink dynamics have been rare in the past literature [13] and continue to be uncommon today [14].

A recent review of source-sink papers found that many studies considered survival or reproduction rates, but movement-exchange rates and patterns were rarely characterized [14]. Dispersal is an important element of source-sink dynamics but is difficult to measure at a scale that is relevant for regional populations [8, 15]. However, without these data, source-sink assessments assume that emigrants die, underestimating survival rates. This simplification can cause an under- or over-valuation of a local population's contribution to regional population dynamics and persistence [3]. The inclusion of immigration data can also help differentiate self-sufficient sources from dependent sources and improve source-sink classifications [16] but is often unavailable [14]. Access to movement information has recently been improved by genetic analyses that assess asymmetric gene flow, immigration, or linkage disequilibrium, and used to infer movement rates and patterns and indicate (but not necessarily confirm) source-sink dynamics [17–19].

Conservation Applications

Source-sink dynamics originated as a theoretical concept; however, the contribution of local-level population dynamics to regional-level population stability has become an important consideration in applied conservation and landscape ecology [14]. Source-sink concepts have contributed to spatial conservation planning and evaluations of the conservation value of resources [8]. Yet, quantitative assessments of source-sink dynamics are uncommon [3, 8, 14] but increasing [20, 21] in applied conservation research. Sites that are presumed to be sources are often prioritized for conservation because they represent productive populations [22, 23]; however, the value of protected sources could be overestimated if they have been misidentified [8, 24, 25]. In some systems, sinks may also be important for metapopulation stability and persistence [26, 27]. Sources and sinks differ in their strength and influence, depending on their quality, extent, and location in a landscape and thus will likely have different conservation values in different contexts [9]. Yet, few analyses have evaluated the contributions of individual sources and sinks to regional population outcomes and management objectives. Exceptions include studies that use contribution metrics [e.g., 3], mechanistic forecasting models [e.g., 23], and simulated patch removal experiments [e.g., 28, 29]. These approaches measure the contribution of local populations to the regional networks, more directly connecting source-sink assessments with conservation and management actions.

Past reviews have surveyed empirical evidence for the existence of sources and sinks or reviewed methods for assessing source-sink dynamics, often focusing on field-based evaluations of terrestrial animal populations [e.g., 3, 8, 14]. In this review, we broadened the frame to examine how source-sink theory and analyses have advanced, as well as the current challenges in using source-sink concepts to support species conservation. Theoretical concepts, source-sink experiments, and species-specific field assessments can all influence conservation decisions. We surveyed this full range of literature and included studies from previously under-represented and non-terrestrial taxa. We aimed to determine the motivation and context behind source-sink studies, as well as the metrics used to determine and characterize source-sink dynamics. To assess the degree to which technological and methodological advances have influenced source-sink studies for focal species, we compared recent and historical trends in a range of systems and taxa, as well as the spatial and temporal scales at which studies were conducted. From our results, we highlight current challenges in applying source-sink theory for species conservation and suggest areas for future expansion of source-sink theory and practice.

Methods

Manuscript Selection

We searched the Web of Science for peer-reviewed journal articles containing the keyword "source-sink" that were published from January 1, 1985, to June 21, 2018. We refined our search by relevant research areas including biodiversity conservation, zoology, forestry, environmental sciences, ecology, fisheries, entomology, mathematics, evolutionary biology, marine freshwater biology, behavioral sciences, oceanography, water resources, and urban studies. To help focus on papers relevant to the dynamics of animal populations, we limited resulting records to papers including at least one of the following key words: population, habitat, dynamics, or conservation. This search yielded 1006 publications that we further screened to include only studies describing the source-sink dynamics of a focal animal species rather than communities of species. Thus, we excluded papers that did not evaluate or discuss animal populations (e.g., papers discussed plant dynamics or carbon sinks), as well as papers evaluating metacommunities, community dynamics, or species diversity and richness ($n = 305$).

We categorized the remaining 701 papers as either *discussing* source-sink dynamics or *using* source-sink theory to structure analyses. Papers discussing source-sink dynamics ($n = 269$) generally linked the concept of source-sink dynamics with study findings or context but did not formally address source-sink theory or concepts in the study questions or methods. These papers frequently used source-sink dynamics as an explanation of patterns in their results but often acknowledged that more evidence was needed to affirm their presence. Papers also discussed looking for source-sink dynamics as a next step in the evaluation of their study system, or as a topic for a future manuscript. We included source-sink reviews, syntheses, and opinion articles in this category. By contrast, we coded papers as using source-sink concepts ($n = 432$) if authors used hypotheses related to source-sink theory or explored source-sink concepts as a central idea in the paper. This category included papers that assessed sources and sinks or expanded or tested source-sink theory.

Manuscript Classification

Papers using source-sink dynamics were classified according to their methodological approach (Fig. 1). Studies were classified as empirical ($n = 283$) if the primary emphasis was on collecting or analyzing organism-specific field data relating to source-sink dynamics. Studies were considered experimental ($n = 22$) if a physical manipulation of a field system or microcosm was undertaken. We defined modeling studies as those that did not collect or rely on system-specific data in source-sink analyses ($n = 127$). This included conceptual, hypothetical, and theoretically oriented papers. Models that heavily relied on empirical data were included as empirical studies.

For papers using source-sink dynamics, we conducted several evaluations, including an assessment of the motivation and context of studies, the characteristics of studied systems and taxa, and the criteria used to evaluate source-sink dynamics. We assessed patterns through time and compared papers published from 1985 to 2012 with recently published studies, 2013–2018.

Motivation and Context

To assess the motivation and context of source-sink studies, we searched all papers that "used" source-sink dynamics for key words that reference the motivation or context of the study: conserv*, manag*, viabil*/viabl*. For papers mentioning one of these variants of conservation, management, or viability, we additionally looked for key words describing the past, current, or potential population trajectory of the focal animal, including declin*, decreas*, equilibrium, stable, growth, and increas*.

System and Taxa Descriptions

We evaluated system type (e.g., terrestrial), taxa (e.g., mammal), location (e.g., North America), habitat type (e.g., wetland), and spatial extent for papers that described real systems, excluding theoretical modeling papers. We coded the spatial extent or scale of each paper as microcosm, local/county, region/state, country, continental, global, island, or unspecified. The local/county scale considered areas as small as parks or other small sites within a city up to entire counties. We coded most national or state parks as local/county unless a quantified area was given. We categorized parks greater than

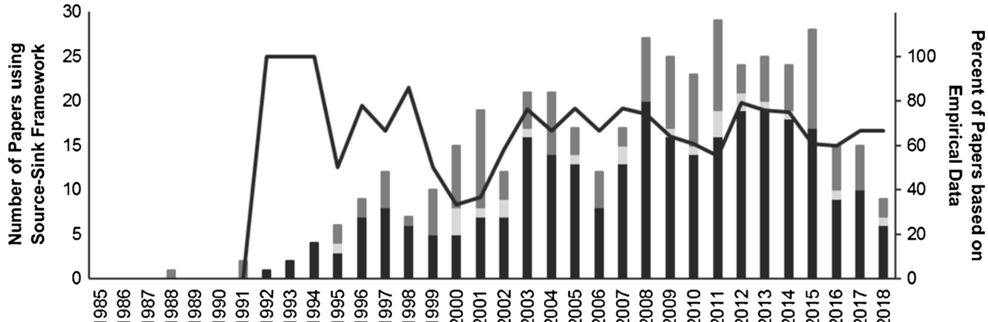

Fig. 1 Distribution of published papers that used source-sink concepts or assessed source-sink dynamics, from 1985 to 2018 ($n = 432$). The number of empirical studies is represented by black bars ($n = 283$), and the black line represents the annual proportion of studies. Modeling studies are indicated by dark gray bars ($n = 125$), and experimental studies are represented by light gray bars ($n = 22$)

20,000 km^2, including the Greater Yellowstone Ecosystem, as a region/state extent. Study extents were categorized as region/state or country if the authors either endeavored to sample or address the focal species' dynamics across the area of a state or country.

Evaluation of Source-Sink Dynamics in Empirical Papers

To further assess how authors identified and evaluated source-sink dynamics, we investigated empirically-based studies in greater detail. We identified whether authors did or did not find evidence of source-sink dynamics in their system. We also noted the types of evidence used to identify source-sink dynamics, including measures of demography, movement, occupancy, habitat selection or habitat quality, growth rates, abundance, density, age structure, body condition, and prey abundance, among others. We evaluated the use of genetic tools in assessments of source-sink dynamics and the types of evidence the genetics data provided (e.g., movement or diversity). Ultimately, we sought to determine how authors assessed source-sink dynamics and the degree to which they considered both demography (reproduction and mortality) and movement (immigration and emigration) in their evaluation of source-sink dynamics.

Results

Publication Trends

The number of published papers using or discussing source-sink dynamics increased from 1985 to the first decade of the twenty-first century. However, the number of source-sink publications declined in recent years (2013–2018; Fig. 1). Studies using source-sink dynamics in model-based analyses remained relatively stable through time. Modeling approaches emphasized mathematical equations, stage-based population models, agent-based simulations, and genetics, along with other modeling methods. The number of empirical studies declined by ~50% (from 19 in 2013 to only 10 in 2017), causing an overall decline in the number of source-sink studies (Fig. 1). The number of empirically based studies generally outnumbered model-based studies, annually comprising ~69% of published papers (1992–2018) after the first empirically based paper was published in 1992.

Population conservation, viability, and management considerations were increasingly used to frame the motivation or context of source-sink studies (Table 1). The majority of papers referred to at least one of these keywords, increasing from 75% (n = 238) from 1985 to 2012 to 87% (n = 101) in the last 5 years (2013–2018). Among papers that refer to a conservation or management context, few studies published through 2012 clearly indicated the current or expected status or trajectory of the regional population (e.g., increasing, stable, decreasing; Table 1), information that could be useful in meta-analyses and making inferences for less studied species and systems. Yet, reporting of population trends increased slightly in 2013–2018 (Table 1). Key words variably described past, current, and future population conditions, increasing uncertainty in classifications of the population state. The most commonly reported population trend was declining (declin* or decreas*, increasing from 50% prior to 2013 to 57% in 2013–2018). Relatively few studies were conducted for increasing populations (growth or increas*; 27% during 1985–2012; 32% during 2013–2018), or stable populations (equilibrium or stable/stabil*; 27% during 1985–2012; 44% during 2013–2018).

Table 1 Motivation and context of source-sink assessments, comparing historical and recent trends

Keyword	1985–2012	2013–2018
N	316	116
Conserv*	59% (n = 185)	71% (n = 82)
Manag*	55% (n = 173)	71% (n = 82)
Viabil*	35% (n = 111)	41% (n = 47)
Papers with conservation, management, or viability context		
N	238	101
Declin*	38% (n = 90)	49% (n = 49)
Decreas*	21% (n = 49)	29% (n = 29)
Equilibrium	14% (n = 34)	11% (n = 11)
Stable/Stabil*	19% (n = 44)	28% (n = 28)
Growth	7% (n = 17)	24% (n = 24)
Increas*	27% (n = 64)	44% (n = 44)

Systems and Taxa

Terrestrial systems were the focus of most early studies that used source-sink concepts (76%; 1985–2012), decreasing to 62% of later studies from 2013 to 2018. We observed complimentary increases in the proportion of marine- (11%) and freshwater-only (8%) studies from (18%) prior to 2013 to 24% and 5% respectively (30%) in 2013–2018 (Fig. 2b). Birds (30%) and mammals (27%) were the most frequently assessed taxa through time (1985–2018; Fig. 2a). However, as the focus of recently published papers shifted from forested terrestrial systems to marine habitats (Fig. 2b; Table 2), the proportion of papers focusing on terrestrial (14%) and aquatic (8%) invertebrates rose substantially (combined; 22% of papers published) from 1985 to 2012 to 11% and

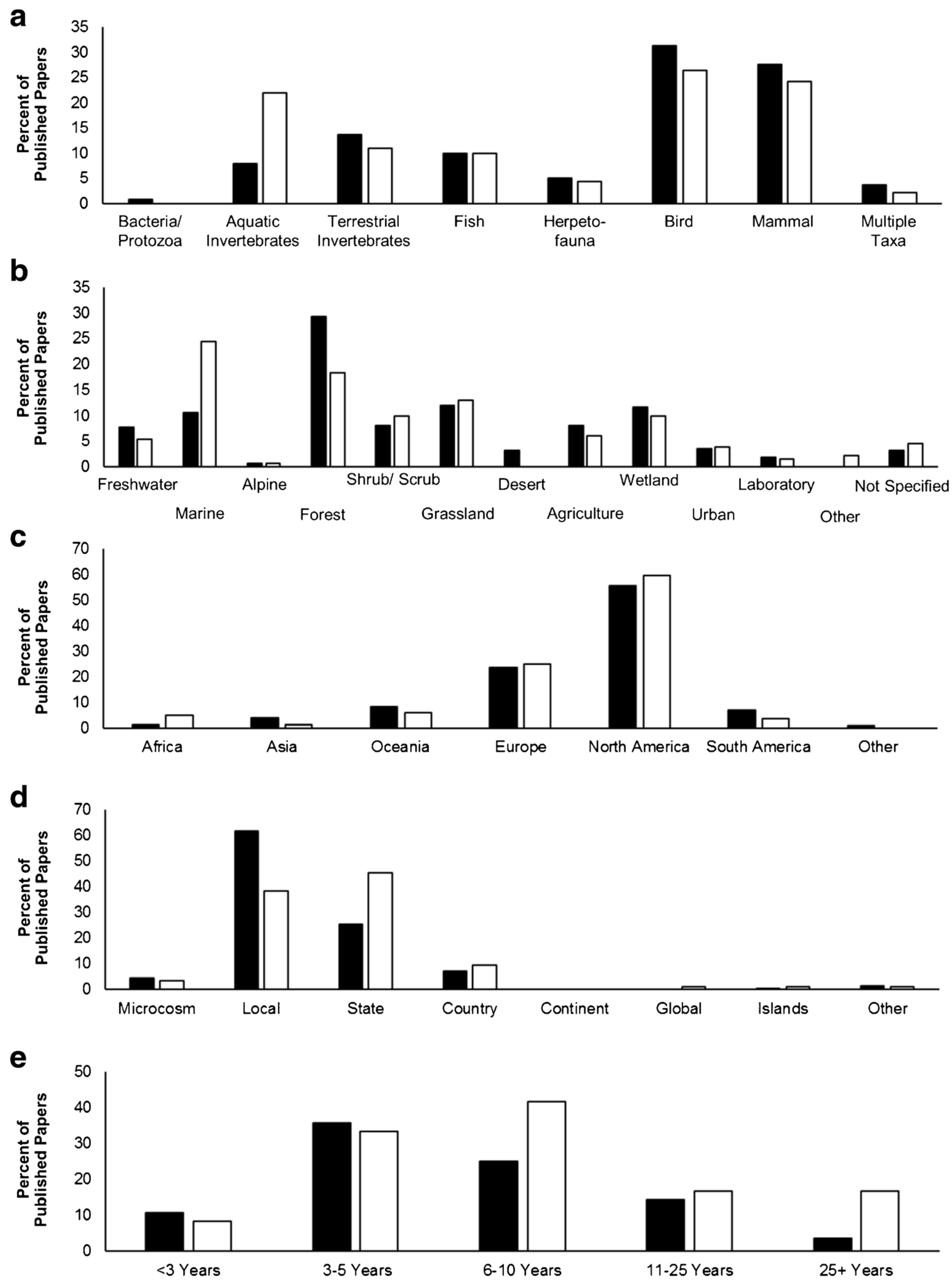

Fig. 2 Taxa (**a**), habitat types (**b**), regions (**c**), and spatial extents (**d**) assessed by studies using source-sink concepts ($n = 432$), and temporal extents (**e**)considered by papers that comprehensively assessed source-sink dynamics using measures of both demography and movement ($n = 38$). Papers published between 1985 and 2012 are represented by black bars and papers published within the most recent 5 years are shown with white bars

22% (combined; 33%) in recent publications (2013–2018; Fig. 2a; Table 2). Most studies were based in North America and Europe, with little representation from other continents (Fig. 2c; Table 2).

Many papers did not report the area of their spatial extent. Of those that did report scale ($n = 318$), most (86%, $n = 274$; 1985–2018) evaluated source-sink dynamics at local or regional spatial extents (e.g., a US county or state), with relatively few studies using smaller (i.e., microcosm) and larger (e.g., countrywide) assessments. Recent studies (2013–2018, $n = 86$) tended to evaluate source-sink dynamics at broader spatial scales than publications prior to 2013 ($n = 212$; Fig. 2d; Table 2). State-level studies represented 45% of papers published since 2013 compared with only 25% of earlier publications. Papers based on the local scale decreased in relative proportion from 62% of papers published before 2013 to 38% of recently published papers (Fig. 2d).

Source-Sink Evaluation

Of 283 papers based on empirical datasets, 79% claimed to find evidence for source-sink dynamics. Of papers making source-sink conclusions, demography and movement were the most commonly used metrics to assess

Table 2 Summary of recent trends (2013–2018) in source-sink studies, relative to 1985–2012

Source-sink study characteristics		2013–2018 trend
# Source-sink papers published		+ 12 papers/year
Papers *using* source-sink dynamics		+ 5.5 papers/year
Using conservation key words		+ 12%
Describing regional population trend		+ 14%
Taxa	Aquatic invertebrates	+ 14%
	Birds and mammals	– 8%
Habitat	Forest	– 11%
	Marine	+ 14%
Region	North America and Europe	+ 5%
	Elsewhere	– 5%
Spatial extent	Local/regional	– 24%
	State	+ 20%
Temporal extent (BIDE papers)	6–10 years	+ 17%
	25+ years	+ 13%
Using births, deaths, immigration, emigration (BIDE)		+ 3.5%/year

source-sink dynamics. The majority of studies (54%) used at least one measure of demography (births alone 9%; deaths 12%; Fig. 3a), and 34% used a combination of births (reproduction) and deaths (mortality). About half of source-sink assessments that considered both births and deaths did not consider any measure of movement (51%; $n = 48$ of 95). Nearly half of all empirical studies assessed at least one measure of movement (Fig. 3b; 50%; $n = 141$), including 21 that solely considered immigration (7%) and 4 that considered only emigration (1%). Forty-one percent of studies ($n = 116$) included both immigration and emigration, of which 58 (50%) did not include demography. Under a third of papers (27%; $n = 76$) considered some combination of demography and movement, but did not consider all BIDE (birth, immigration, death, emigration) measures.

Only 13% ($n = 38$) of studies comprehensively assessed source and sinks by including both births and deaths as well as immigration and emigration (Fig. 3c). This low proportion was relatively consistent through time, with a slight increase (3.5% per year) in the last half decade (Fig. 3c). The majority (87%; $n = 33$) of the comprehensively assessed papers found evidence for source-sink dynamics within their study system. Abundance or density metrics were additionally considered in nearly half (42%; $n = 16$) of the comprehensively assessed papers, but genetic data were used in only one paper that conducted a complete BIDE assessment.

We were able to assess the timeframe for 35 (92%) of papers that comprehensively assessed sources-sink studies. The majority used datasets from a relatively limited timeframe, with 51% of papers $n = 18$ drawing from input datasets of five (or fewer) years (Fig. 2e). Recent studies (2013–2018; $n = 12$), however, tended to use longer datasets. Comprehensive source-sink assessments based on 6–10 years of data became more frequent in the last 5 years, increasing from 25% of papers, $n = 7$, published before 2013 to 42% of recent publications, $n = 5$. The use of long-term datasets (> 25 years) also increased from only 4% prior to 2013 to nearly 17% of papers published in the past 5 years.

Although demography and movement are the classic measurements required to assess source-sink dynamics, nearly a quarter of studies (23%; $n = 64$) assessing sources and sinks did not use a single demographic or movement metric. Of these, 48 papers (75%) concluded that they found evidence for the presence of source-sink dynamics. Instead of using demography or movement, these papers used a variety of alternative measures to support their conclusions, including one or more metrics of occupancy (31%; $n = 20$), abundance (44%; $n = 28$), density (33%; $n = 21$), growth rates or body size (13%; $n = 8$), and habitat quality or selection (28%; $n = 18$). Other metrics, including age/stage structure, sex ratios, body condition, patch size and connectivity, prey/food availability or consumption rates, predator density or abundance, parasites density or parasitism rates, community measures such as species richness, and phenological matching, were also considered by 25 papers (39%; Fig. S1). Genetic analyses were used in 64 publications from 1985 to 2018 (23%; Fig. 3d) to assess diversity (19%), movement (dispersal, gene flow; 16%), effective population size (4%), and population structure and relatedness (4%; Fig. S2). The first paper to use genetic techniques to help assess source-sink dynamics in our data set was published in 1993. The use of genetics proportionally increased (~ 1.23% per year thereafter), stabilizing in the past 5 years and comprising nearly 36% of published papers from 2013 to 2018 (Fig. 3d).

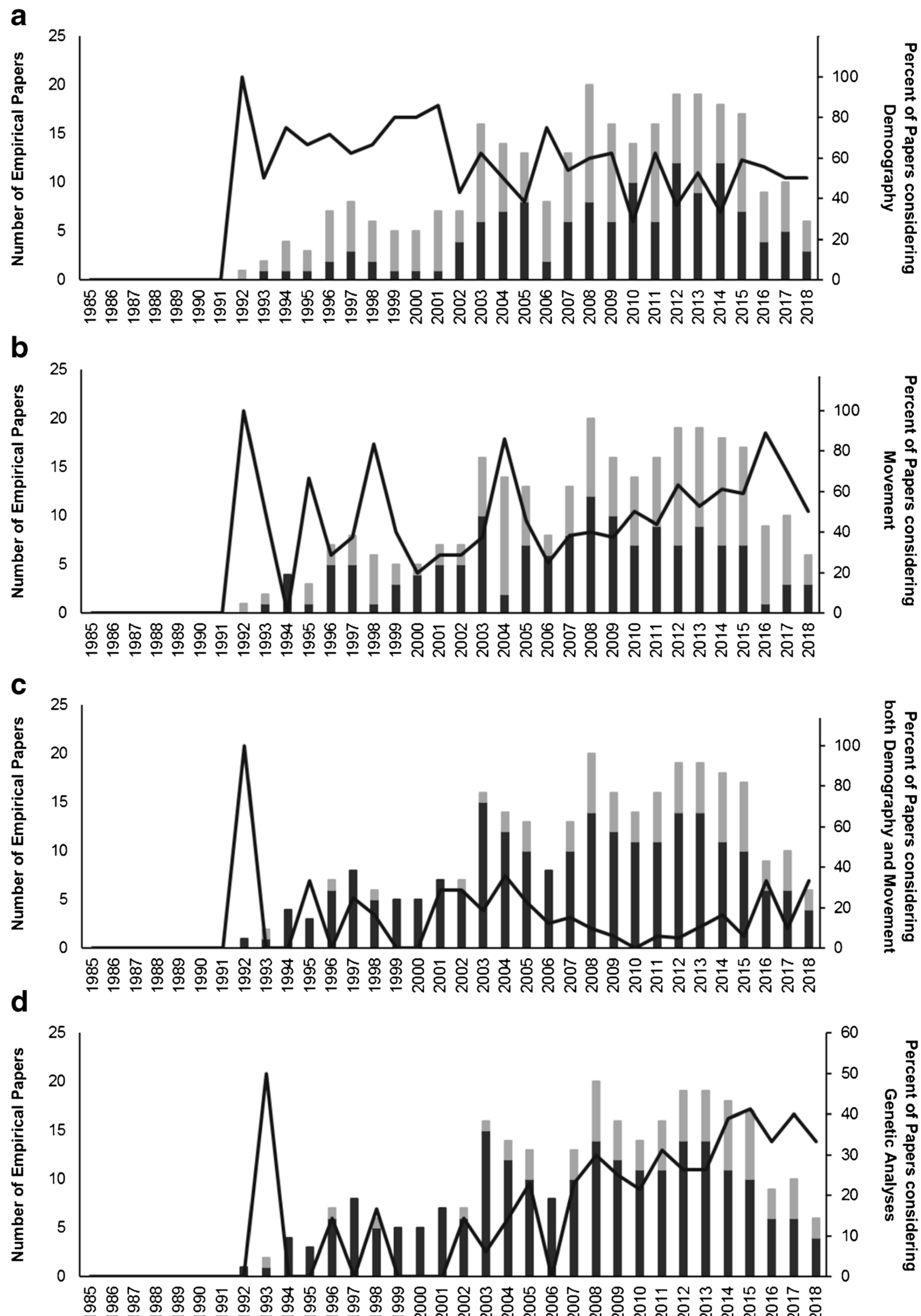

Fig. 3 Proportion of empirically based source-sink papers (n = 283; black line) that used at least one measure of (**a**) demography, (**b**) movement, (**c**) comprehensively assessed source-sink dynamics by considering births, deaths, immigration, and emigration, or (**d**) used genetic techniques in their analyses. Gray bars represent the number of papers using a given type of data, whereas the black bars describe the number of papers that did not use the specific type of data

Discussion

An overwhelming majority (~ 80%) of quantitative source-sink assessments found support for source-sink dynamics, seeming to support the premise that sources and sinks are plentiful in heterogeneous landscapes. However, the majority of empirical studies that identified sources and sinks did so based on limited data and largely untested inferences. Only a tenth of studies used all four metrics—survival, reproduction, emigration, and immigration—as per classical source-sink equations [1, 30] and most studies used short time series. This disconnect between the expectations of source-sink theory and the current realities of empirical data collection undermines robust assessments of sources, sinks and their prevalence in nature.

Nearly a third of studies relied on metrics that are expected to be weak or inconsistent indicators of source-sink status such as abundance or density [3, 14]. Source-sink literature is replete with cautions of omitting demographic or movement data and relying on untested assumptions that density or local abundance indicate population productivity [12, 31, 32]. However, it is often difficult and/or costly to obtain demographic and movement data. Despite the fact that technological improvements have reduced the cost and increased the ease at which some data is collected (e.g., genetics, movement), even in our sample of the most recent studies, only a small proportion of studies were able to collect the requisite field data. Greater technological advancements, as well as cost reductions, may be required to see demographic and movement data used in the majority of empirical source-sink assessments. Even so, quantifying demographic and movement rates will always be somewhat resource-intensive and unlikely to be undertaken for many taxa and across large spatial extents. Rules of thumb or robust simplified metrics could help guide decisions in less studied systems, when action is required and empirical data is insufficient [8], but should be evaluated as data become available [33].

The expansion of source-sink spatial and temporal analysis extents may have been helped by technological advances in recent years. Efficiencies in tracking and mapping organisms may have contributed to a shift from local to broader spatial extents, enabling source-sink assessments at the landscape- and species-levels. Similarly, comprehensively assessed papers that include BIDE are increasingly incorporating longer time series of data. As source-sink status can vary over time [34–36] as a result of stochasticity, assessments of source-sink dynamics that use multiple years of data are more likely to provide robust conclusions. Directional changes in environmental conditions [e.g., anthropogenic changes to habitat, management actions; 36, 37] or population conditions (e.g., invasion, disease, or interspecific competition) can also influence source-sink dynamics. This complicates assessments based on short-term data and could invalidate prior source-sink assessments [38]. Although uncommon, we found some studies that used long time series or empirically based models to assess or project changes in habitat and population conditions. These longer time series facilitated the exploration of the effects of stochastic and directional change on source-sink status [e.g., 39]. Studies collecting long time series of data can adaptively re-assess source-sink dynamics and more robustly support population conservation and prioritization decisions.

Framing source-sink results in the context of key population and habitat attributes, including regional population trend, is an important step towards developing a general understanding of the dynamics of non-equilibrium populations and identifying conservation actions that consistently support persistence. However, we found that source-sink studies did not consistently describe key habitat (i.e., composition and structure) and population conditions (i.e., regional population trends). Further, studies seldom or inconsistently reported measures of habitat quality or modification (e.g., the magnitude of development, land use change) across patches/populations. Although source-sink research is increasingly conducted in the context of species conservation, many papers did not clearly express their motivations, making it difficult to assess the degree to which source-sink studies were designed and intended to inform species conservation.

Source-sink analyses are increasing their relevance for management and conservation by extending the classical mathematical theory designed for simple equilibrium populations [1] to accommodate the realities of declining or growing populations living and moving in complex environments [10, 40]. Empirical and modeling studies are testing common methods and yielding new approaches to evaluating sources and sinks for challenging and less traditional source-sink systems. For example, some papers tackled species with complex life histories [e.g., 41], long-distance migration [e.g., 42], regional movement among seasonal habitats [43], and diffuse rather than discrete habitat patches [23]. Applied source-sink modeling studies are now weighing the different strengths, sizes, and locations of sources and sinks to prioritize populations for conservation [3, 10, 20]. A few papers forecast source-sink dynamics by building and comparing scenarios wherein stressors (e.g., climate and land-use change) [42], habitat restoration, or population-recovery actions influence the long-term status of sources and sinks [28, 38, 43].

Conclusions

Source-sink theory and practice have matured and become increasingly relevant for species conservation and management. Despite the recent decline in the number of source-sink papers, there are many important avenues for future expansion to improve our knowledge of spatially structured populations in heterogeneous landscapes. In particular, we lack a good understanding of the conditions under which limited data (metrics, spatial, and temporal scales) can defensibly support source-sink assessments and be scaled up to the extent at which management decisions are made. We have also shied away from quantitatively assessing the value of specific sources and sinks for managing population outcomes such as regional population stability or persistence. Given the challenges of supporting long-term demographic and movement studies at broad spatial and temporal extents, we need synthetic research that identifies the range of population and landscape conditions under which rules of thumb are appropriate (e.g., equilibrium populations in simple and static landscapes). Importantly, we need new theory to devise general, yet testable, hypotheses for declining species inhabiting complex, atypical, and dynamic landscapes. Targeted meta-analyses and realistic landscape-population models, such as spatially explicit individual-based models, will be instrumental in devising new hypotheses. Although a small number of studies take on these non-traditional populations and complicated environments, there are many unresolved challenges that require much more research effort and funding resources to solve.

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Author Contributions JH, JL, and LW conceived of the study and developed the methods. LW, JH, KM, and AB reviewed and evaluated papers. JH, LW, JH, and NS wrote the manuscript.

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Compliance with Ethical Standards

Conflict of Interest On behalf of all authors, the corresponding author states that there is no conflict of interest.

Human and Animal Rights and Informed Consent This article does not contain any studies with human or animal subjects performed by any of the authors.

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