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Quantifying ecosystem service flows at multiple scales across the range of a long-distance migratory species

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A B S T R A C T

Migratory species provide ecosystem goods and services throughout their annual cycles, often over long distances. Designing effective conservation solutions for migratory species requires knowledge of both species ecology and the socioeconomic context of their migrations. We present a framework built around the concept that migratory species act as carriers, delivering benefit flows to people throughout their annual cycle that are supported by the network of ecosystems upon which the species depend. We apply this framework to the monarch butterfly (*Danaus plexippus*) migration of eastern North America by calculating their spatial subsidies. Spatial subsidies are the net ecosystem service flows throughout a species' range and a quantitative measure of the spatial mismatch between the locations where people receive most benefits and the locations of habitats that most support the species. Results indicate cultural benefits provided by monarchs in the U.S. and Canada are subsidized by migration and overwintering habitat in Mexico. At a finer scale, throughout the monarch range, habitat in rural landscapes subsidizes urban residents. Understanding the spatial distribution of benefits derived from and ecological support provided to monarchs and other migratory species offers a promising means of understanding the costs and benefits associated with conservation across jurisdictional borders.

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1. Introduction

Seasonal wildlife migration connects distant ecosystems and people in a predictable way. Because of this regular movement, the presence of a migratory species in any one portion of its range is dependent, in part, upon favorable conditions in other portions of its range. Similarly, the benefits people receive from a species in one location depend on habitat in other parts of its migratory range in addition to the local habitat where the species is encountered. Spatial subsidies are a quantitative metric describing the net difference between the amount of benefits received from a species in a given area and the amount of benefits supported by habitat in the same area (López-Hoffman et al., 2013; Semmens et al., 2011). A spatial subsidy measures the degree to which the provision of

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benefits (i.e., ecosystem services, the benefits provided by nature to people; MEA, 2005) by a species in one location is subsidized by ecological conditions and processes supporting the species in other locations. As such, spatial subsidies are a specific example of the more broadly defined concept of telecoupling, which refers to environmental and socioeconomic interactions over distances (Liu et al., 2013; López-Hoffman et al., 2017a,b).

Ecosystem service (ES) benefits are carried by flows of matter or information such as water or scenic views (Villa et al., 2014). In the case of ES provided by migratory species, the animals themselves are fundamental to flows between regions. The ability to describe, quantify, and map such flows can facilitate the application of ES concepts to policymaking because values are more readily understood in terms of benefits accrued to specific beneficiary groups and locations (Villa et al., 2014). Spatially explicit information on flows of ES thus provides a convenient means of incorporating both technical/biological factors and social/economic factors in sustainable natural resource management—a critical component of analyses of complex social-ecological systems (Bennett et al., 2017; Berkes et al., 2008; Ostrom, 2009).

Scale mismatches—a mismatch between the extent and resolution of management actions and the ecological system of interest—are a common problem in conservation planning (Guerrero et al., 2013) and in particular for the management and conservation of migratory species (Berkes, 2006). Migratory species conservation is complex, often involving competing objectives, multiple actors across multiple management jurisdictions, and many possible conservation actions. Management decisions made at national and sub-national scales often do not match the scale of the ecological processes relevant to the conservation problem. Approaches and tools accounting for the multi-scale nature of conservation problems are needed to address scale mismatches that arise during the various stages of conservation planning (Guerrero et al., 2013) and can impede effective implementation of migratory species conservation.

We present an approach based on ES flows to synthesize the biological and socioeconomic information involving migratory species. The spatial subsidies approach addresses the need to account for the multi-scale nature of migratory species conservation problems embedded in complex, broad-scale social-ecological systems. The approach was developed as way to quantify the value of specific habitat for the role it plays in supporting migratory wildlife and the ES they provide, as well as to indicate management actions, such as payments for ecosystem services (PES), that could be employed to incentivize conservation when local incentives are otherwise lacking. The ability to define the regions used in a spatial subsidies analysis to align with ecological, jurisdictional, or other socioeconomic boundaries permits the consideration of ES flows between regions best suited to inform different types of management decisions. For example, it may be useful to consider flows between countries, or perhaps between rural and urban areas within a country. We use the case of the monarch butterfly (*Danaus plexippus*) migration of eastern North America to explore how the spatial subsidies approach can be used to quantify net flows between and within regions and discuss implications for migratory species management and conservation.

1.1. Monarch butterfly case study

The monarch butterfly is an iconic North American insect characterized by a spectacular and highly visible annual migration across the continent, from winter aggregations in central Mexico to summer breeding habitat extending well into southern Canada. The annual migration can take as many as five generations to complete and directly exposes millions of people to the monarch's life cycle. Numerous studies have documented the importance of monarchs to people, which is reflected in their willingness to donate to and engage in monarch conservation efforts (Diffendorfer et al., 2014), volunteer for monarch citizen science (Ries and Oberhauser, 2015), visit overwintering sites (Brenner and Job, 2006), and organize diverse partnerships across social boundaries for monarch conservation (Gustafsson et al., 2015).

The monarch population has undergone a precipitous decline over the last two decades (Semmens et al., 2016; Vidal and Rendón-Salinas, 2014). This decline is partly attributed to logging activities and the associated degradation of macro- and micro-climatic conditions at the overwintering sites in central Mexico (Brower et al., 2016; Honey-Rosés, 2009; Shahani et al., 2015; Vidal et al., 2014). Habitat loss due to changing agricultural practices in the U.S. has also been implicated (Flockhart et al., 2015; Pleasants and Oberhauser, 2013; Oberhauser et al., 2017; Pleasants, 2017; Saunders et al., 2017), and other factors may also be contributing (Inamine et al., 2016; Ries et al., 2015; Thogmartin et al., 2017a), such as climate (Saunders et al., 2017) or disease (Altizer et al., 2000). Monarchs lay eggs on many species of milkweed (*Asclepias* spp.) that developing larvae require for food. Declines in milkweed abundance are well documented and highly correlated with the adoption of herbicide-tolerant genetically modified corn and soybeans (Pleasants and Oberhauser, 2013), which now constitute 92% and 94% of these crops, respectively, in the U.S. (Fernandez-Cornejo, 2015). To date, conservation action has focused on the restoration of grassland ecosystems in rural areas, which provide both milkweed and other nectar resources for monarchs. Previous research has suggested that the amount of habitat restoration needed to stabilize the monarch population at a level capable of withstanding natural population fluctuations will require engaging private landowners in agricultural landscapes (Thogmartin et al., 2017b).

The monarch population decline and correspondingly elevated risk of losing the eastern monarch migration (Semmens et al., 2016) have galvanized support for conservation across North America, with the Presidents of Mexico and the U.S. and the Prime Minister of Canada agreeing in 2014 to devise a plan for saving the continent's monarch butterfly migration (Baker and Malkin, 2014). Understanding where conservation efforts are needed from an ecological perspective has been the traditional focus of migratory species conservation efforts. However, the multi-national conservation effort for monarchs also raises important questions about who will benefit most from conservation investment, who will be negatively impacted (e.g., the opportunity cost of habitat protection), and how to balance the costs and benefits of conservation across a species' migratory range. The spatial subsidy approach represents the first quantitative means of addressing these questions within the context of migratory species conservation. We use the monarch case study to explore how subsidies (net ES flows) can vary in relation to the spatial configuration of social and ecological boundaries.

2. Materials and methods

2.1. Quantifying flows

The spatial subsidy approach (López-Hoffman et al., 2013; Semmens et al., 2011) was designed to quantify the *net* flow of benefits, as valued goods and experiences (Chan et al., 2012), between regions encompassing the full range of a migratory species. It is based on the concept that migratory species are partially dependent upon all parts of their range, so benefits received in any one region are sourced from the entirety of the range. In effect, all regions both receive benefits from and provide benefit to all regions within their range. These gross benefit flows are conceptualized as migration support provided by location i *out* to other locations (M_{Oi}), migration support received at location i *in* from other locations (M_{Ii}), and migration support from location i received *locally* at location i (M_{Li}). These are defined as:

$$M_{Oi} = (V_{\bullet} - V_i)D_i$$

$$M_{Ii} = V_i(1 - D_i)$$

$$M_{Li} = V_i D_i$$

where $V_{\bullet}$ is the total annual value of all ES provided by a species throughout its range and V_i is the total annual value of ES provided at location i. D_i is the proportional dependence of a species or subpopulation on location i, which is defined as the extent to which a location contributes to the overall viability of a migratory population. Values for D_i must satisfy the following two requirements:

$$0 \leqslant D_i \leqslant 1$$

$$\sum_{i=1}^{m} D_i = 1$$

where D_i represents the proportional dependence at any given location, and i encompasses all m locations utilized by a species. These requirements reflect the fact that migratory species, like all species, are 100% dependent upon their environment. Below, we describe how the D_i and V_i parameters were estimated throughout the full migratory range of the eastern population of the monarch butterfly.

Gross flows out of and into each part of the migratory range (i.e., migration support) can be subtracted to calculate the *net* flow of benefits to/from each location, which we define as the spatial subsidy, Y_i:

$$Y_i = M_{Oi} - M_{Ii} = V_{\bullet}D_i - V_i$$

This is a measure of the difference between the benefits received and benefits provided by any given location. Positive values indicate the location is, on net, subsidizing other areas and negative values indicate the location is being subsidized by other areas. When applied to all m locations throughout a species range, this equation satisfies the requirement that the sum of all subsidies is zero, or

$$\sum_{i=1}^{m} Y_i = 0$$

Any number of regions can be used in this analysis and they can be defined in any way, so long as they encompass the migratory range of the species, are consistent throughout the analysis, and permit estimation of the requisite value and proportional dependence parameters.

In addition to the net flow of ES into or out of each region (Y_i), there are also net benefits received and supported locally. The net local flow (Y_{Li}) is the net flow of benefits from ecosystems to people *within* each region. This intraregional flow represents the net amount of benefits supported by the habitat in each region. When a region is providing a subsidy (i.e., $Y_i \geq 0$), the habitat in the region supports all the benefits received locally (V_i) in addition to exporting some to other regions. For receiving regions, the net local flow is equal to the benefits received locally less the amount of the subsidy received by the region.

$$\left.\begin{array}{l} Y_{Li} = V_i + Y_i \\ Y_{Li} = V_i \end{array}\right\} \begin{array}{l} \text{if } Y_i < 0 \\ \text{if } Y_i \geqslant 0 \end{array}$$

The sum of Y_i values greater than zero (i.e., the net flow of ES from providing to receiving regions) plus all Y_{Li} values is equal to the total value provided by a species ($V_{\bullet}$), thus completing the picture of how all ES from migratory species flow to beneficiaries throughout their range.

$$\sum_{i=1}^{m} Y_i > 0 + \sum_{i=1}^{m} Y_{Li} = V_{\bullet}$$

To quantify gross ES flows between any two specific regions, we rely on two important considerations: (1) all regions both provide migration support to and receive migration support from all other regions within the migratory range of the species; and (2) the amount of migration support provided or received is a function of proportional dependence and the value received in each region. The gross outgoing flow of migration support from region a to region b is equal to the value received from a species at location b that depends on habitat for the species at location a. Conversely, gross incoming migration support from region b to region a is equal to the value received from a species at location a that depends on habitat for the species at location b.

$$M_{O_{\overrightarrow{ab}}} = M_{Oa}\frac{V_b}{(V_{\bullet} - V_a)};\ M_{I_{\overleftarrow{ab}}} = M_{Ia}\frac{D_b}{(1 - D_a)}$$

Which simplifies to:

$$M_{O_{\overrightarrow{ab}}} = D_a V_b;\ M_{I_{\overleftarrow{ab}}} = V_a D_b$$

Net flows only occur from regions providing subsidies (i.e., $Y_i > 0$) to regions receiving subsidies (i.e., $Y_i < 0$). Here, we assume that each region providing a subsidy will do so in proportion to the magnitude of the subsidies in the receiving regions. For example, the net flow between region a ($Y_a > 0$) and region b ($Y_b < 0$) can be calculated as:

$$Y_{\overrightarrow{ab}} = Y_a \frac{Y_b}{\sum_{i=1}^{m} Y_i < 0}$$

2.2. Estimating proportional dependence

Our D_i calculations were derived from a spatially explicit Bayesian hierarchical analysis of a demographic matrix model that included five regions (Mexico Wintering, Mexico Migration, South, North Central, and Northeast) and migration between them (Oberhauser et al., 2017; Fig. 1). A perturbation analysis (Caswell, 2000) was used to evaluate the relative importance of the five different model regions. For each region, we simultaneously increased all of the vital rates (fecundity and survival) for that region by 5% and recorded the new mean population growth rate, λ, relative to the baseline model. For the South model region where breeding takes place in both spring and fall, seasonal differences in vital rates necessitated separate simulations for each season. D_i values were calculated by normalizing the percent changes in λ such that they summed to one across all regions, a requirement of the D_i parameter (Semmens et al., 2011).

2.3. Estimating economic values

The value of monarch butterflies to people living within their migratory range is not a direct result of any market goods or services they provide—monarchs have little value when collected, do not pollinate commercial crops, and do not control any pest species. Their value instead derives from non-market cultural ES, which include their contributions to the non-material benefits (e.g., capabilities and experiences) arising from human-ecosystem relationships (Chan et al., 2012). A comprehensive, bottom-up approach to identifying and valuing the many specific cultural benefit types people derive from monarch butterflies

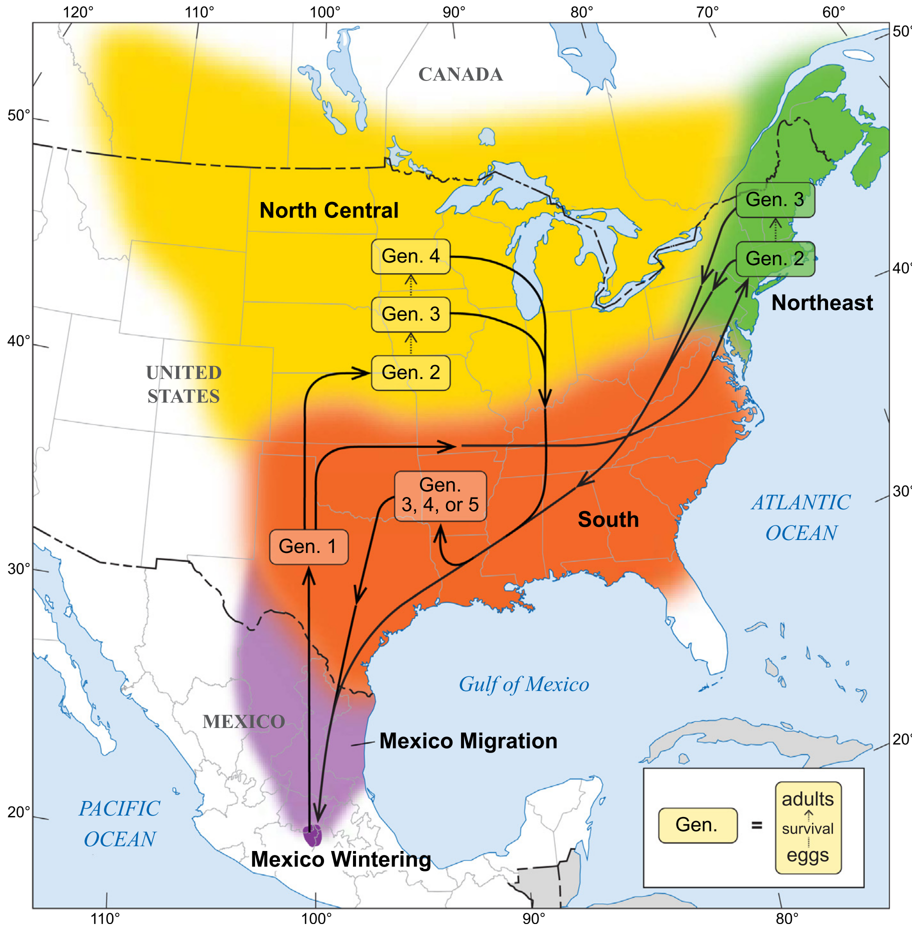

Fig. 1. Map of the monarch butterfly annual migration in eastern North America. Superimposed on the map is the conceptual model encoded in the demographic model. The five model regions labeled in bold type on the map also represent the five locations used in the subsidy calculations. Modified from Oberhauser et al. (2017).

throughout their range would be the most complete means of deriving the economic values needed for applying the spatial subsidies framework. Without the funding to adopt this approach, however, we instead relied on several aggregate measures of value that were more readily available: willingness to pay (WTP) for monarch conservation, time spent volunteering for monarch-related citizen science, and participation in tourism focused on viewing monarch butterflies. These measures provide a reasonable indication of the value provided by monarchs, but do not distinguish specific benefit types (such as aesthetic, spiritual, learning, or bequest) and may therefore miss certain benefits. The values for each measure were estimated separately in each model region for our V_i calculations, with the specific methods used for each value type described separately below. We are mindful of the difficulty of estimating monetary values for these non-material benefits and do not intend to suggest that these values could be paid in compensation for the loss of a species.

2.3.1. Volunteer time

We use the value of volunteer time in a novel way—as an indication of the value people derive from cultural ecosystem services. Each year, volunteers donate tens of thousands of hours to monarch-focused citizen science efforts throughout North America (Ries and Oberhauser, 2015). Though we do not know with which specific non-material benefit types this donation is associated (e.g., bequest, learning), it stands to reason that time spent volunteering for monarchs likely results from such benefits and is therefore a useful indicator of part of the value that volunteer citizen scientists receive from monarchs.

Volunteer hours for monarch-focused citizen science were compiled by Ries and Oberhauser (2015) across 11 different monarch-centric monitoring programs in North America. To assign a value to this time, we obtained data on the value (in U.S. dollars, hereafter USD) of a volunteer hour from Independent Sector, an organization tracking and publishing information about volunteerism and its value in the United States, for all U.S. states (Independent Sector, 2015). Independent Sector calculates these values by averaging the hourly earnings across all production and non-supervisory workers on private, non-farm payrolls and increasing it by 12 percent to estimate for fringe benefits. We obtained values for volunteer time in Canada from Statistics Canada for 2011 (Statistics Canada, 2015). Statistics Canada does not report wage rates separately for different sectors, so we used its raw mean hourly wage data for each province. Lacking hourly wage rate data for Mexico, particularly at the state level, we used 2008 per capita state-level GDP data from the Instituto Nacional de Estadística y Geografía (INEGI) to derive a coarse estimate of hourly wage rates. All values were converted to USD using the Penn World Tables (Feenstra et al., 2013) and to 2014-equivalent values using Bureau of Labor Statistics' (BLS) Consumer Price Index (CPI) Inflation Calculator (BLS, 2015) to correspond with the stated WTP values described in the following section.

Volunteer hours across Canada, the U.S., and Mexico were summarized to degree blocks in a GIS (Fig. 2a). Using this 1-degree point GIS layer, we assigned each point to: (1) its appropriate province or state and (2) its appropriate region from the monarch demographic model. We multiplied the total volunteer hours for each point by the appropriate state or provincial volunteer wage

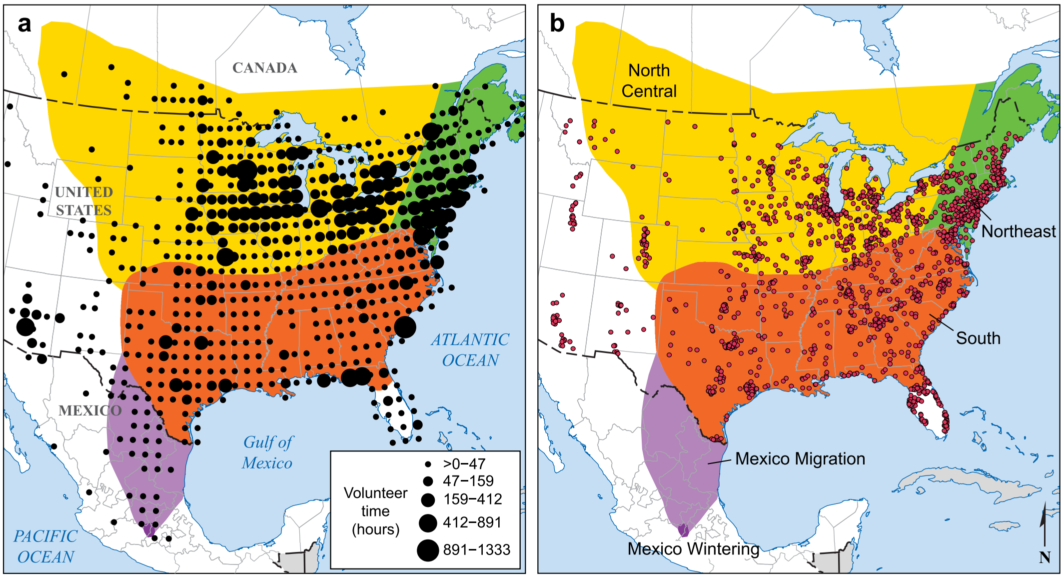

Fig. 2. Maps showing (a) the spatial distribution of monarch-centric volunteer time and (b) the locations of willingness-to-pay survey respondents used to estimate values in each of the five model regions. Points outside the colored regions were not used in the analysis.

rate. This yielded a total value of volunteer labor for each point. We then split the points across the five monarch model regions and summed the values for each region.

2.3.2. Willingness to pay

Economists (Farrow and Zerbe, 2013; Loomis, 2002; Sassone and Schaffer, 1978) and U.S. government agencies (U.S. Environmental Protection Agency, 2010; U.S. Water Resources Council, 1983) have long used WTP as a measure of the benefits that individuals receive from a good or service, whether marketed or non-marketed. Although the term "willingness to pay" conjures up to some a "fanciful" measure of value and to others a benefit measure highly constrained by income, neither concern is quite correct. WTP for another unit of market goods is the good's price. WTP for public goods, such as the benefits provided by monarchs, reflects the maximum amount of money a person would pay for an increase/improvement or to avoid a reduction in these benefits (Loomis, 2002). While WTP is bounded by income, as we show below income has an extremely small effect on WTP for monarch protection. Asking individuals their maximum WTP is appropriate when trying to obtain a species' existence and bequest values as there is no directly observable behavior as there is for volunteerism or tourism (Richardson and Loomis, 2009).

The data on WTP for monarch conservation were obtained via a national survey of U.S. households in 2012 (Diffendorfer et al., 2014). The online survey of ~2000 randomly selected households (Fig. 2b) was designed to provide a stratified random sample that was demographically and economically representative of all U.S. households. It asked questions about willingness to donate to conserve monarch habitat. Responses were used to estimate total one-time WTP by model region in the U.S. portion of the monarch's range. These values were then annualized to correspond to the other values in the subsidy calculation by dividing total WTP by 33—the difference between the average life expectancy in the U.S. and the average age of survey respondents—and then converted to 2014-equivalent USD using the Bureau of Labor Statistics' CPI Inflation Calculator (BLS, 2015) for consistency across all value types.

To derive WTP estimates for the Canadian and Mexican portions of the monarch's range, we followed best practices for international value transfer (Ready and Navrud, 2006). We regressed household income against total WTP and found the effect of household income, though statistically significant, was weak and extremely small (β = 1.59E-005, $p < 0.0001$, $R^2 = 0.0141$). As a result, we used the U.S. mean household WTP, adjusted for purchasing-power parity, to estimate WTP for households in Canada and Mexico. Assuming a uniform value for household WTP does not allow for regional variation in the cultural value of monarchs, but there is no evidence suggesting differences in the cultural importance of monarchs between the U.S. and Canada or Mexico.

2.3.3. Tourism

Economic benefits of monarch-related tourism are mainly limited to the overwintering region in central Mexico. Most of the land in the overwintering region is controlled by ejidos (communal agricultural land), indigenous communities, and private owners. Community groups collect fees from visitors for entrance, parking, and horse transportation to monarch colony sites. In addition, they run concessions to augment their income from monarch-related tourism. Brenner and Job (2006) provide the only published accounting of the total direct income from tourism in the overwintering region, which they estimated to be $2.2M from entrance fees and tourism for the winter of 2004–2005. Although this number predates our other value estimates by 7–8 years and does not include indirect income, it is the only available estimate. We converted to 2014-equivalent USD using the Bureau of Labor Statistics' CPI Inflation Calculator (BLS, 2015).

2.4. Estimating rural versus urban contributions

To demonstrate how the spatial subsidy approach can be adapted to provide information relevant to management at different social and ecological scales, we estimated the subsidy between rural and urban landscapes. This involved partitioning our previous proportional dependence and value estimates for each monarch region between rural and urban areas. Sufficient data to do this quantitatively were only available for part of one region, the U.S. portion of the North Central region, for which we describe the methods below and provide results as an illustrative example.

To partition proportional dependence and value estimates, we estimated the fraction of total milkweed and that of the human population within urban areas. We used an Urban Areas/Clusters dataset (U.S. Census Bureau, 2010) to identify those areas classified as urban and to estimate their total human population. Polygons from this dataset were then used to clip out urban areas from the Cropland Data Layer (USDA, 2016) land-cover map for the north-central U.S. pertinent to the mapping of milkweed habitat (Rohweder and Thogmartin, 2015). A systematic literature review was used to obtain empirical estimates of common milkweed (*Asclepias syriaca*) stem densities associated with each cover class (Thogmartin et al., 2017b). Stem density estimates were then applied to the land-cover map to estimate total milkweed stems; the clipped land-cover map yielded the fraction of total milkweed stems in urban areas.

Quantitative estimates of the presence of milkweed, the monarch's sole food source during the larval stage, were used as a proxy for monarch habitat and thus to partition the model-derived proportional dependence of monarchs between urban and rural portions of the region. The fraction of human population living in urban versus rural portions of the landscape was used to partition the value derived from monarchs, as this value represents cultural ES received by the beneficiaries where they reside. We assumed equal per-capita value for monarchs between the residents of urban and rural areas.

In the remainder of the range, we applied the same proportions for D_i and V_i that we found for the North Central region. Although urbanization rates and the distribution of habitat between rural and urban areas are likely to be similar throughout the monarch range, this extrapolation is for illustrative purposes only. We intend it to demonstrate how the subsidy calculation can be refined to provide information on subsidies and associated ES flows with greater spatial resolution when sufficient data are available.

3. Results

3.1. Proportional dependence

The perturbation analysis with the demographic model revealed the South to have the greatest influence on overall monarch population dynamics, with a proportional dependence of ~35% (Table 1). Together, the three regions hosting reproduction (South, North Central, and Northeast) were responsible for 84% of the total D_i values for monarchs.

3.2. Volunteer time

Almost 34,000 h of monarch-centric volunteer time were logged across the monarch's migratory range in 2011 (Ries and Oberhauser, 2015), with a total value of almost $750,000 (Table 1). Almost all volunteer time originated in the U.S. and Canada, with more than half of the total hours logged in the North Central region. Citizen science is not prevalent overall in Mexico (although this is changing) and not permitted in some areas.

3.3. Willingness to pay

Mean household WTP for monarch conservation ranged from $40 in the Northeast region to $27 in the overwintering region in Mexico. Multiplying these values by the number of households in each region yields a one-time WTP of over $3.5B across the monarch's range, which is consistent with the numbers reported for the U.S. by Diffendorfer et al. (2014). Annualized values totaled over $125M across the monarch's range, with the large majority (>80%) originating in the U.S. where most people living in the monarch's range are located (Table 1).

3.4. Tourism

Converted to 2014 USD, the Brenner and Job (2006) estimate of annual total direct income from tourism at the monarch overwintering sites is approximately $2.8M (Table 1). The remaining regions where no organized, fee-based tourism occurs show zero values for this value type.

3.5. Spatial subsidies

Spatial subsidy results vary substantially depending on how the regions are defined spatially. Using the five model regions (Fig. 1), defined based on the monarch's seasonal life stages, the regions receiving the most benefits (highest V_i values) are also those most important to the viability of the monarch population (highest D_i values). The North Central and Northeast regions receive slightly more benefits than they support and the Mexican regions support slightly more than they receive, but the total subsidy across the range amounts to only about 10% of the annual benefits provided by monarchs—about US$13M (the sum of positive subsidy values; Table 2).

The monetary values in Table 2 represent the gross and net value of ES flows between and within the regions of the monarch's migratory range. Gross flows include the value supported by each region that is received elsewhere (M_{Oi}), the value supported elsewhere that is received in each region (M_{Ii}), and the local value supported by habitat in each region (M_{Li}). Gross ES flows to/from/within each region are presented separately in Fig. 3, maps *a* through *e*, with each map showing the gross flows for one region. Net benefit flows include the subsidies between regions (Y_i) and the net benefits supported by habitat within each region (net local flow, Y_{Li}) and are presented in Fig. 3f. The smaller number of net ES flows shown in Fig. 3f result after the more numerous gross flows cancel each other out, allowing net flows to be shown in their entirety throughout the migratory range in one map. Viewed in this manner, the regions largely support the benefits they receive, resulting in the relatively small net flows between regions.

3.5.1. Rural–urban subsidies

When the monarch regions are further subdivided to separate source and delivery areas by distinguishing urban and rural areas, the magnitude of the subsidies (net interregional flows, Y_i)

Table 1
Proportional dependence (D_i) and annual value (V_i) estimates for each monarch region. Values are presented in USD per year, rounded to the nearest $100.

	D_i	WTP	Tourism	Volunteer	V_i
Mexico Wintering	0.08	$244,600	$2,777,400	$0	$3,022,000
Mexico Migration	0.08	$5,018,900	$0	$400	$5,019,300
South	0.354	$43,956,100	$0	$182,000	$44,138,100
North Central	0.282	$44,996,800	$0	$418,400	$45,415,200
Northeast	0.204	$29,959,700	$0	$172,800	$30,132,500
Total	1	$124,176,100	$2,777,400	$773,600	$127,727,000

Table 2
Components of the spatial subsidy and flow calculations. Values are presented in USD per year, rounded to the nearest $100.

	Gross outgoing migration support, M_{Oi}	Gross incoming migration support, M_{Ii}	Gross local migration support, M_{Li}	Net subsidy, Y_i	Net local flow, Y_{Li}
Mexico Wintering	$9,976,400	$2,780,300	$241,800	$7,196,100	$3,022,000
Mexico Migration	$9,816,600	$4,617,700	$401,500	$5,198,900	$5,019,300
South	$29,590,500	$28,513,200	$15,624,900	$1,077,300	$44,138,100
North Central	$23,211,900	$32,608,100	$12,807,100	-$9,396,200	$36,019,000
Northeast	$19,909,300	$23,985,400	$6,147,000	-$4,076,100	$26,056,300
Total	$92,504,700	$92,504,700	$35,222,300	$0	$114,254,700

increases substantially. Approximately 98.7% of all milkweed stems are located in areas classified as rural by the U.S. Census Bureau, whereas these same areas contain just 12.3% of the human population. Because of this difference, rural landscapes are consistently subsidizing benefits in urban areas throughout the monarch range. Though difficult to present in mapped form because urban regions are not contiguous, the results in Table 3 show that the total net flow between regions (sum of all positive Y_i values) amounts to almost 85% of the annual benefits provided by monarchs ($V_{\bullet}$), in contrast to just 10% between the original five model regions.

4. Discussion

The monarch butterfly migration results in flows of cultural ES throughout eastern North America. Analyzing these benefit-flows from source to delivery areas has revealed differences in the net flow of ES at different spatial scales. Calculating spatial subsidies is a means of quantifying differences between the amount of benefits a region supports (through habitat maintenance) and the amount of benefits it receives (through ecosystem goods and services) from a migratory species. The geographic regions used in spatial subsidy calculations can be defined in any way (national, subnational, physiographic, etc.), provided the regions encompass the migratory range of the species and requisite parameters can be estimated for each region (Semmens et al., 2011). As such, it is possible to structure regions to inform management and policy at multiple spatial scales, from local to regional.

For benefits provided by the monarch butterfly, primary source and delivery areas happen to largely coincide when the regions are defined according to the monarch's seasonal life history. As a result, the calculated subsidies (US$13M) are small relative to the total annual value of US$127M provided by monarchs, but they do indicate that social welfare (as derived from WTP, volunteer time, and tourism values) in the U.S. and Canada is subsidized by migration and overwintering habitat in Mexico. At this scale, the spatial subsidy calculation can inform coordinated international management strategies by providing an indication of the relative levels of national investment that may be appropriate for migratory species conservation. For instance, our results suggest conservation payments from the U.S. and Canada to Mexico could help offset opportunity costs associated with habitat protection on private land in the monarch winter range, which in turn would promote the persistence of value received by individuals in the U.S. and Canada.

The spatial coincidence of the most important habitat and greatest benefit delivery seen in this example is not always the case; López-Hoffman et al. (2017b) found a much larger divergence, and correspondingly elevated subsidies, across the range of Mexican free-tailed bats. Similarly, when the monarch regions are defined according to both seasonal life history and habitat to intentionally separate providing and receiving regions, the magnitude of the subsidies increases substantially. Separating out major habitat (rural) and beneficiary (urban) areas resulted in total net ES flows (subsidies) of more than US$107M across the monarch range. That around 85% of the annual benefits provided by monarchs are supported by rural habitat conservation and stewardship is a key reframing of the question of monarch habitat conservation, particularly in the U.S. and Canada. Rural landowners are commonly portrayed as having contributed to the monarch population decline rather than as carrying the responsibility, and incurring the cost, of maintaining habitat that, on net, benefits urban populations.

The linkage, or teleconnection, between monarch habitat in rural grasslands and socioeconomic benefits in cities represents a new means of understanding benefits associated with habitat restoration efforts in rural areas, particularly when combined with the numerous other benefits provided by grassland ecosystems (e.g., water quality regulation, crop pollination, carbon sequestration, and ecological support for many other wildlife species). Payments for ES from urban to rural areas have been suggested as a means to alleviate rural poverty, improve environmental conservation in rural areas, and transform harmful production subsidies into helpful payments for environmental conservation (Gutman, 2007). They could also play an important role in increasing monarch habitat restoration on agricultural land, which is necessary to meet monarch conservation targets (Thogmartin et al., 2017b) and will require productive engagement with agriculture (Landis, 2017).

Given the many sources of uncertainty in our calculations, at this time we do not recommend the quantified subsidies be interpreted as actual amounts "owed" by or to any region. However, our approach provides the only available means of estimating quantitative differences between the benefits that specific landscapes and habitats provide for migratory wildlife and the ES those species provide to people living in other locations. This framing may help people understand that the benefits they enjoy from migratory wildlife are often supported by habitat in other regions. To the extent that providing wildlife habitat is recognized as possibly coming at a price to providers (or providing regions) in the form of foregone economic opportunities, an understanding of spatial subsidies has the potential to suggest management alternatives suitable to achieving conservation objectives across jurisdictional boundaries.

The data needed to apply the spatial subsidies approach includes demographic information sufficient to develop a spatially explicit population model for the species in question, as well as socioeconomic information on the benefits provided by the species to people throughout its range. Demographic information is expensive and time consuming to collect due to the fieldwork it requires, but these data are routinely collected for species of conservation concern. Socioeconomic information on the value of benefits provided by migratory species are more readily available when markets exist, such as for harvested species, but are rarely compiled throughout a species range. For non-market benefits such as those considered in the present study, systematically engaging stakeholders throughout the migratory range to conduct a comprehensive valuation of the specific benefits derived from a

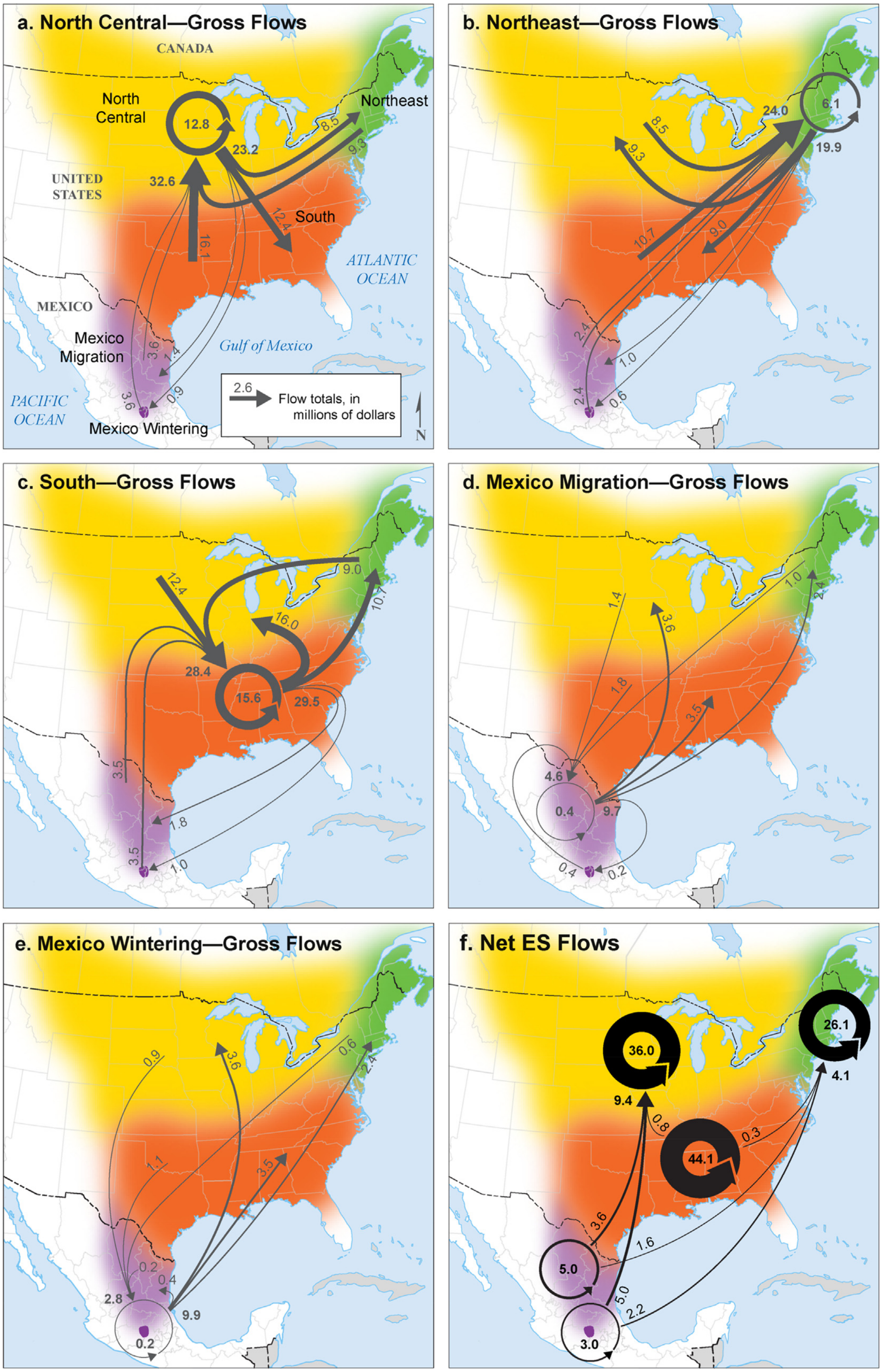

Fig. 3. Maps showing (a–e) the gross flows of ES to/from/within each of the five model regions independently and (f) the net flow of ES provided by monarchs throughout North America. Arrows, and their width, represent the magnitude of interregional flows of ES value in millions of dollars per year from providing to receiving regions, with circular arrows indicating intraregional flows. In Fig. 3a–e, gross intraregional flows are equivalent to the local migration support M_{Li} value for each region; gross interregional flows are derived from outgoing (M_{Oi}) and incoming (M_{Ii}) migration support columns in Table 2. In Fig. 3f, intraregional flows are derived from the net local flow (Y_{Li}) column in Table 2; interregional net flows are the spatial subsidies (Y_i). The sum of all net ES flows is equal to $V_{\bullet}$—the total annual value provided by monarchs.

Table 3
Components of the spatial subsidy and flow calculations, partitioned between rural and urban areas. Results for urban areas are highlighted in bold text. Values are presented in USD per year, rounded to the nearest $100.

	D_i	V_i	M_{Oi}	M_{Ii}	Y_i	Y_{Li}
Mexico Winter	0.080	$3,022,000	$9,976,400	$2,780,300	$7,196,100	$3,022,000
Mex. Mig. rural	0.079	$615,400	$10,036,700	$566,800	$9,470,000	$615,400
Mex. Mig. urban	**0.001**	**$4,403,900**	**$128,300**	**$4,399,400**	**−$4,271,100**	**$132,800**
South rural	0.349	$5,411,300	$42,736,900	$3,520,600	$39,216,200	$5,411,300
South urban	**0.005**	**$38,726,700**	**$409,600**	**$38,548,500**	**−$38,138,900**	**$587,800**
North Central rural	0.278	$5,567,900	$34,001,000	$4,018,200	$29,982,900	$5,567,900
North Central urban	**0.004**	**$39,847,300**	**$322,200**	**$39,701,200**	**−$39,379,100**	**$468,200**
Northeast rural	0.201	$3,694,200	$24,973,800	$2,950,400	$22,023,400	$3,694,200
Northeast urban	**0.003**	**$26,438,200**	**$268,600**	**$26,368,100**	**−$26,099,500**	**$338,700**
Total	1	$127,727,000	$122,853,400	$122,853,400	$0	$19,838,500

species is likely to be cost prohibitive in most situations. However, commercially available services for conducting internet-based valuation surveys similar to the Diffendorfer et al. (2014) WTP study are relatively affordable, fast, and can be translated into multiple languages. If these data were more routinely collected, spatial subsidies information could be developed and incorporated into conservation planning for many migratory species of conservation concern.

5. Conclusions

Spatial subsidies integrate ecological and socioeconomic information to provide a quantitative measure of the net flow of ES benefits between regions encompassing the full range of a migratory species. Aligning regions with different types of boundaries (e.g., political, social, or ecological) provides a means of applying the spatial subsidy framework to address scale mismatches in conservation planning by providing information on the costs and benefits associated with migratory species conservation at different spatial scales. For monarch butterflies, we demonstrated that migration and overwintering habitat in Mexico subsidizes the delivery of approximately $13M in cultural ES benefits in the U.S. and Canada annually. In addition, monarch habitat in rural areas subsidizes a large majority of all cultural ES benefits provided by monarchs and delivered to urban residents throughout the migratory range. The linking of ecological source and social delivery areas in this fashion can help identify management and policy strategies balancing the conservation of migratory wildlife and preservation of human welfare.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at https://doi.org/10.1016/j.ecoser.2017.12.002.

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