ARTICLE IN PRESS

Ecosystem Services xxx (2018) xxx–xxx

Contents lists available at ScienceDirect

Ecosystem Services

journal homepage: www.elsevier.com/locate/ecoser

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

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ARTICLE INFO

Article history:
Received 2 June 2017
Received in revised form 17 November 2017
Accepted 5 December 2017
Available online xxxx

Keywords:
Biodiversity conservation
Political ecology
Social-ecological systems
Spatial subsidies
Telecoupling
Monarch butterfly

ABSTRACT

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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https://doi.org/10.1016/j.ecoser.2017.12.002
2212-0416/Published by Elsevier B.V.

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