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Research, part of a special feature on Programme on Ecosystem Change and Society (PECS): Knowledge for Sustainable Stewardship of Social-ecological Systems | Department of Applied Research and Agricultural Extension, Madrid Institute for Rural, Agricultural and Food Research and Development (IMIDRA), 2Socio-Ecological Systems Laboratory, Department of Ecology, Universidad Autónoma de Madrid, 3Centro de Estudios e Investigación para la Gestión de los Riesgos Agrarios y Medioambientales, Universidad Politécnica de Madrid, 4Environmental Change Institute, University of Oxford, 5Laboratorio Analítico Biotécnico, Parque Científico Tecnológico de Almería, 6Andalusian Center for the Assessment and Monitoring of Global Change, Department of Biology and Geology, Universidad de Almería, 7Department of Biological Sciences, Idaho State University ABSTRACT Biophysical and social systems are linked to form social-ecological systems whose sustainability depends on their capacity to absorb uncertainty and cope with disturbances. In this study, we explored the key biophysical and socio-cultural factors underlying ecosystem service supply in two semi-arid watersheds of southern Spain. These included variables associated with the role that freshwater flows and biodiversity play in securing the system's capacity to sustain essential ecosystem services and their relationship with social demand for services, local water governance, and land-use intensification. Our results reveal the importance of considering the invisible dimensions of water and biodiversity, i.e., green freshwater flows and trait-based indicators, because of their relevance to the supply of ecosystem services. Furthermore, they uncover the importance of traditional irrigation canals, a local water governance system, in maintaining the ecosystems' capacity to supply services. The study also highlights the complex trade-offs that occur because of the spatial mismatch between ecosystem service supply (upstream) and ecosystem service demand (downstream) in watersheds. Finally, we found that land-use intensification generally resulted in losses of the biophysical factors that underpin the supply of some ecosystem services, increases in social demand for less diversified services, and the abandonment of local governance practices. Attempts to manage social-ecological systems toward sustainability at the local scale should identify the key biophysical and socio-cultural factors that are essential for maintaining ecosystem services and should recognize existing interrelationships between them. Land-use management should also take into account ecosystem service trade-offs and the consequences resulting from land-use intensification. Key words: demand; freshwater flow; interaction; irrigation community; land-use intensification; social-ecological system; social preference; spatial pattern; trait-based indicator It is widely recognized that ecosystems directly or indirectly contribute to human well-being through the supply of vital ecosystem services (MA 2005, Diaz et al. 2006). The Millennium Ecosystem Assessment (, the Economics of Ecosystems & Biodiversity (, and the Intergovernmental Platform on Biodiversity & Ecosystem Services () have brought the ecosystem services concept into broader environmental planning and policy arenas. This has been possible because of the development of new conceptual and analytical frameworks that analyze the complex relationships between biophysical and social systems (Ban et al. 2013). These frameworks recognize that biophysical and social systems are interdependent and form social-ecological systems (SESS; Liu et al. 2007, Ostrom 2009). Ostrom (2007, 2009) developed a general framework to explore sustainability through the analysis of interdependencies and complex linkages in SESS. This study adapts Ostrom's framework to empirically conceptualize two Mediterranean semi-arid watersheds as SESS (Fig. 1). Under this framework, different subsystems are identified: the biophysical system and its related ecological processes (i.e., the freshwater flows and biodiversity that underlie the supply of ecosystem services in semi-arid watersheds), the supplied ecosystem services, the system's users (i.e., the beneficiaries who generate ecosystem service demand), and the governance system (i.e., local water governance). All are jointly affected by different drivers of change (Fig. 1). This framework is a useful tool for assessing associations, i.e., trade-offs or synergies, between ecosystem services while also assessing interactions between the factors that generate and influence the provision of ecosystem services. For example, it allows the study of (1) supply-supply trade-offs where the provision of one or several services compromises the provision of others and supply-supply synergies where ecosystem services are provided concurrently; (2) demand-demand trade-offs between beneficiaries where the demand for one or various ecosystem services negatively affects the interest of needs of other stakeholders and demand-demand synergies where stakeholders share a common interest; and (3) supply-demand trade-offs/synergies where there is a temporal or spatial mismatch/match between ecosystem service supply and the derived social demand (Mouchet et al. 2014). Different authors have remarked on the necessity of conducting research focused on ecosystem service associations to properly implement the concept into real conservation and management actions (Howe et al. 2014). It can help to identify and promote management strategies that are able to enhance a flow of ecosystem services simultaneously (Raudsepp-Hearne et al. 2010); highlight the consequences of difficult management decisions (McShane et al. 2011); and improve understanding of the functioning of ecological processes that are important for service supply and the drivers of change that affect them to avoid unexpected changes (Bennett et al. 2009). However, the majority of studies to date have focused on single services (Seppelt et al. 2011, Mitchell et al. 2013) or one-to-one relationships; studies considering several ecosystem services are urgently required (Bennett et al. 2009, Howe et al. 2014). Moreover, although knowledge on the role of biodiversity for the supply of ecosystem services is improving (Cardinale et al. 2012), few empirical studies have focused on understanding the social-ecological processes that underpin services (Bennett et al. 2009, Lavorel and Grigulis 2012) and the effects of governance decisions and environmental change on their supply (Harrison et al. 2014). Semi-arid systems in the Mediterranean Basin have been identified as areas where water resources and biodiversity have significantly deteriorated (García-Ruiz et al. 2011, Lorenzo-Lacruz et al. 2012), with important consequences for ecosystem service supply and human well-being (Safriel and Adeel 2005, Spanish NEA 2014). In this sense, good management of freshwater flows (runoff or blue water flow and evapotranspiration or green water flow) and biodiversity is essential for the supply of provisioning (e.g., freshwater, food for human consumption), regulating (e.g., water quality, erosion control), and cultural (e.g., local identity, recreational activities, spiritual values) services, which all contribute to human needs (Diaz et al. 2006, Brauman et al. 2007, Willaarts et al. 2012). As was found by Martín-López et al. (2012), people appreciate the ecosystem services obtained from watersheds in semi-arid systems highly and manage these systems based on their knowledge and perception of the factors affecting service supply. However, different stakeholders hold different social perceptions regarding the importance of individual ecosystem services, which can result in potential trade-offs between beneficiaries. Furthermore, certain stakeholders possess higher levels of power in relation to land-use management so that their knowledge and interests drive land-use changes, with consequences in the ecosystem services supply (Niesta-Arandia et al. 2014). During the last 60 years, land-use change in the Mediterranean has been characterized by the abandonment of farming in marginal rural areas and the intensification of agriculture in valleys and flat areas (Aznar-Sánchez et al. 2011). These strategies have contributed to local socioeconomic development, but at the same time they have also affected ecosystem service supply and the landscape configuration (Vidal-Legaz et al. 2013). This study aims to identify the connections between biophysical and socio-cultural factors in two semi-arid watersheds in the Mediterranean Basin to explore key factors underlying ecosystem service supply and the sustainability of SESS at the local scale. Our specific objectives were (1) to assess the relationships between biophysical and socio-cultural factors underpinning ecosystem services supply and the effect of land-use intensification as a key direct driver of change in the region and (2) to explore the spatial pattern of these interactions and the resulting spatial trade-offs in ecosystem service supply and demand along the watersheds. To address these objectives, we analyzed (see Fig. 1) the biophysical factors underpinning ecosystem services in terms of blue and green freshwater flows and variables related to riparian vegetation and aquatic macroinvertebrates; the supply of ecosystem services and their social demand, in terms of importance and, in
terms of local water governance factors in ecosystem services supply and demand; and the associations among these three factors and land-use intensification. We furthermore visualized the spatial pattern of these interactions and the resulting spatial trade-offs (supply-demand). The complexity of linkages in SESS requires approaches that are able to integrate the whole range of interactions between subsystems (Fig. 1). It also requires studies that assess trade-offs at relevant spatial scales, which will depend on where a particular service is supplied, demanded, and managed, and when trade-offs could emerge. As shown by Howe et al. (2014), many trade-offs emerge at the local scale, because stakeholder interests are usually at this scale. Thus, we made a special effort to collect primary and secondary data at the local scale to obtain reliable assessments of the key factors that generate and influence the provision of ecosystem services. This also enabled the interactions between these factors to be tested. In this context, the current study illustrates an application of social-ecological, place-based research as it contributes to the advancement of knowledge on the associations between biophysical and socio-cultural factors that drive ecosystem service interactions in the European semi-arid region. Therefore, we seek to draw attention to the importance of interdisciplinary research at the local scale for understanding the complexities behind ecosystem service interactions and, in turn, to contribute to the Programme on Ecosystem Change and Society (). STUDY AREA We conducted this study in two semi-arid watersheds, conceptualized as SESS: the Adra and the Nacimiento, both located in the Almería and Granada provinces in southeast Spain (Fig. 2). Both watersheds are part of the so-called Andalusian Mediterranean River Basin district. The Adra watershed drains an area of 742 km² and has a population of 55,601 inhabitants distributed across 14 municipalities. The Nacimiento watershed, a natural corridor bordered by two mountainous massifs, has a drainage area of 598 km², has 12,305 inhabitants in 10 municipalities, and is the upper part of the Andarax watershed. The headwaters of the two watersheds are located in the Sierra Nevada Protected Area, which is the highest mountain range in the Iberian Peninsula, whereas the lowlands are characterized by having a marked Mediterranean semi-arid climate. Despite sharing a common and homogeneous history that provides both watersheds with a marked agrarian character, more recent development processes, especially since the 1950s, have led to considerable differentiation of upstream and downstream regions. In general terms, the upper mountainous areas are still characterized by subsistence farming, mostly dedicated to growing olive and almond trees on terraces, and have recently experienced a strong process of depopulation. In contrast, the lower areas with milder climates (mainly in the Adra watershed) have developed competitive, intensive greenhouse horticulture (Aznar-Sánchez et al. 2011), which not only has led to the overexploitation of aquifers and water and soil pollution, but also has created several social conflicts (Sánchez-Piçón et al. 2011, Quintas-Soriano et al. 2014). In previous studies, both watersheds were divided into homogeneous geographical sectors (four in the Nacimiento watershed and three in the Adra watershed; Fig. 2) using a set of economic, demographic, social, resource-use, and land-use variables, and performing multivariate statistical analyses; see Niesta-Arandia et al. (2011) for more details. The four geographical sectors of the Nacimiento watershed, N1, N2, N3, and N4, are arranged in a west-east gradient. N1 represents municipalities in the Granada province, which are characterized by the highest altitude (more than 1000 miles above sea level) and are mainly devoted to livestock, cereal crops, and olive and almond orchards. N2 represents the Upper Nacimiento of the Almería province municipalities, which are dedicated to olive and almond tree orchards. N3 represents the intermediate Nacimiento, which is characterized by a younger population with a higher level of formal education and an economy devoted to new land-uses and service sector jobs. N4 represents the lower Nacimiento, which contains the municipalities with the oldest population and the lowest depopulation. The three geographical sectors of the Adra watershed, A1, A2, and A3, are arranged in a north-south gradient. A1 represents the Upper Adra, which contains several municipalities that are protected under the Sierra Nevada Protected Area and therefore have significant territory dedicated to forest landscapes and some tourism, e.g., snow tourism and hiking. A2 represents municipalities in the Cofrades mountains, which are characterized by livestock production, almond and olive orchards, and vineyards. A3 represents the lower Adra, which is focused on intensive agriculture in greenhouse farms that supports a higher population density. This geographical zoning was taken into account in the data compilation and analysis of all the factors described in this study. METHODS Hydrological factors of blue and green freshwater flows were used as key biophysical factors related to the supply of ecosystem services in watersheds. We refer to blue freshwater flow as the surface runoff or groundwater flow feeding rivers, lakes, or wetlands and to aquifers and green freshwater flow as the soil moisture evapotranspired by vegetation (see Table 1). Falkenmark and Rockström (2004) blue water flows generate well-known ecosystem services, such as freshwater for human consumption, irrigated croplands, the maintenance of habitats for aquatic biodiversity, and aquatic recreation activities. Green water flows have been commonly associated with provisioning services such as food production because the rainfall infiltrated and stored in the soil supports the primary productivity required for agricultural activities; however, they also generate numerous regulating and cultural services (Willaarts et al. 2012). To assess the blue and green freshwater flows within each of the two watersheds, we used the eco-hydrologic model BalanceMED (Willaarts et al. 2012). BalanceMED is a semideterministic model that can be used to quantify the mean hydrological flows of Mediterranean watersheds using long-time series of monthly rainfall and potential evapotranspiration. The model is spatially explicit and provides monthly outputs of both blue and green freshwater flows. To quantify the effect of biodiversity on ecosystem service supply, we measured a traditional metric of diversity, the Shannon-Weaver diversity (H; Shannon 1948) for riparian vegetation and aquatic macroinvertebrates (Table 1). In addition, we analyzed functional indicators because it is recognized that functional composition has the most important effect on ecosystem service supply among all components of biodiversity (Diaz et al. 2006). We measured the trait-based indicators identified in previous studies as potentially useful predictors of key ecosystem processes for ecosystem service supply, with a focus on riparian and aquatic vegetation (Diaz et al. 2007, García-Llorente et al. 2011) and aquatic macroinvertebrates (Archambault et al. 2010, Vandewalle et al. 2010). Both biological communities play an important role in maintaining water quality and erosion control: two main elements of the ecological functioning in semi-arid environments (Armas et al. 2011, Castro et al. 2014). Riparian and aquatic plants with complex root architecture enhance soil stability and erosion control, whereas water quality depends on nutrient retention as mediated by traits such as leaf area, growth form diversity, and decomposability (Diaz et al. 2007, De Bello et al. 2010, García-Llorente et al. 2011). Furthermore, macroinvertebrates are key indicators for assessing water quality (Cheimonopoulou et al. 2011). For example, macroinvertebrates with shredders' feeding habits have bioturbation potential to improve nutrient mobilization and water quality (De Bello et al. 2010). Even though functional traits have been previously examined (Usseglio-Polatera et al. 2000), explicit associations among traits and ecosystem services are not yet well documented for macroinvertebrates (De Bello et al. 2010). However, in this study, our intention was to focus on those trait-based indicators that have been shown to have the capacity to denote ecosystem service supply rather than on particular functional groups attached to particular services. Different indices have been proposed to measure the functional traits of a community, but there is no consensus about which factors are most suitable (Casanoves et al. 2011). In this study, to avoid the richness effect, we used the functional dispersion index (FDis, Table 1), which is the mean distance in multidimensional trait space of individual species to the centroid of all species. It includes species abundances by shifting the position of the centroid toward the more abundant species and weighting distances of individual species by their relative abundances (Laliberté and Legendre 2010). This index is also used to measure response diversity, which is defined as the species' ability to persist in the face of environmental changes. Riparian vegetation and macroinvertebrates were sampled at 24 points throughout both watersheds. All biological data were obtained in the spring (April 2009) to avoid possible seasonal differences in results due to the wide seasonal changes in Mediterranean rivers (Williams 2005). Sample points for biological factors are shown in Figure 2. Appendix 1 provides a description of the sample points and the list of traits and their subdivision into attributes used to calculate the functional dispersion index. Ecosystem services: supply and social demand We considered the ecosystem service supply and the social demand for
ecosystem services in terms of importance or use. The selection of ecosystem services was based on the key services in the study area, the need to cover all categories of ecosystem services, and the availability of data in accessible data sources, such as official statistics. Overall, we compiled information on provisioning (food from traditional agriculture and freshwater), regulating (erosion control and water quality), and cultural (ecotourism) services. Food from traditional agriculture, freshwater, and erosion control have been found to be critical in the area because they were perceived as both important for social well-being and vulnerable to loss or degradation (Niesta-Arandia et al. 2014). These services are highly related to the agrarian and semi-arid characteristics of the study area, which are directly affected by the land-use change taking place, i.e., land-use intensification near the coast and abandonment in the mountains (Castro et al. 2014, Quintas-Soriano et al. 2014). Both selected regulating services are also important in the context of water constraints and relief impediments, because water quality and erosion control act as intermediate services to the supply of provisioning ones, i.e., freshwater and food from agriculture. Finally, previous studies in the semi-arid region of Spain have highlighted the important role of ecotourism and recreational activities in local communities, in terms of both welfare and well-being (García-Llorente et al. 2012). The data about the supply of food from traditional agriculture, erosion control, and ecotourism were obtained from the Andalusian Multi-territorial Information System (, using as variables traditional agricultural area, the percentage of area with low erosion, and the number of bedroom places in rural hotels and hotels, respectively (Table 1). To measure the water quality of rivers and streams in both watersheds, we used macroinvertebrate data. Macroinvertebrate community structure has been commonly used for the environmental assessment of aquatic systems because of its demonstrated role as a water quality indicator (Sánchez-Montoya et al. 2010). Here, we estimated the Iberian Biological Monitoring Working Party index for water quality (Alba-Tercedor and Sanchez-Ortega 1988, Alba-Tercedor et al. 2002) because it has been widely used to assess the ecological status of surface water bodies and because it allows the actual composition of the biological community to be compared with predefined reference conditions (Munné and Prat 2009, Sánchez-Montoya et al. 2010). Quality levels (high, good, moderate, poor, and bad) were calculated based on Hydrological Planning Technical Guidance (IPH 2008), i.e., the Spanish legal instrument supporting the implementation of the EU Water Framework Directive. Finally, the freshwater supply was interpreted following the blue water figures obtained from the hydrological factors described above (Table 1). To analyze the importance of the target ecosystem services to society, direct face-to-face questionnaire surveys were conducted in the study area between May 2009 and February 2010. The sampled population was selected randomly, with the aim of covering a wide range of ecosystem service beneficiaries, including residents in the study area, workers, and tourists. Only individuals over 18 years old were interviewed, and the total sample was made up of 381 respondents. The sampling was conducted at 34 different sampling points in the study area, including protected area offices, urban zones, city halls, agrarian offices, recreational areas, and agricultural fields (Fig. 2). The questionnaires included a question about the ecosystem services that were highly demanded by people because of their importance for human well-being. Each respondent selected the most demanded ecosystem services from a list with examples and pictures of the ecosystem services provided by the study area (for more details, see Appendix 2). The list contained the main ecosystem services supplied in the study area, following the information collected from interviews and previous studies (MA 2005, Spanish NEA 2014). We then calculated from the questionnaires (1) which ecosystem services were highly demanded in terms of the number of respondents (expressed as a percentage) who selected them from the list (a service was considered important when it was named by more than 20% of respondents) and (2) the demand scores (expressed as a percentage) of the five selected ecosystem services (i.e., traditional agriculture, freshwater, water quality, erosion control, and ecotourism, independently of the percentage of respondents selecting them). Appendix 2 shows the questionnaire content and structure, and the list of ecosystem services presented. The question was extracted from a broader questionnaire conducted in a previous research project in the study area (for more details see Niesta-Arandia et al. 2014). The social importance of freshwater as expressed in the questionnaires was complemented by an indicator of freshwater consumption compiled from the Regional Ministry of Agriculture, Fisheries and Environment of the Government of Andalusia (CAPMA 2010) and Martínez-Rodríguez (2011). Local water governance factors The availability of several water-related ecosystem services such as freshwater availability and water quality is linked with the use of traditional irrigation systems that use water canals and ditches because these systems manage interseasonal water availability by infiltrating and storing water in land (Pulido-Bosch and Ben Shih 1995). To assess the importance of local water governance factors in the dynamics of SESS, we explored the role of traditional irrigation canals (hereafter called the acequia system) and their management (Meinzen-Dick 2007). The acequia system was one of the first methods used for irrigation and artificial recharge of aquifers in the Iberian Peninsula, and their use dates back to the Muslim period (Pulido-Bosch and Ben Shih 1995). Acequias divert water away from snowmelt and the supplying river to allow gravity-fed irrigation of the downstream floodplain corridor for agriculture. This system has been traditionally governed by local organizations that manage the distribution of water. The main role of these irrigation communities is to facilitate conflict resolution, local control, and a just and equitable distribution of water resources (Maass and Anderson 1978). Here, we analyzed water governance using the following variables: the acequias conservation status (very good/good, regular, deteriorated/abandoned) and the number of traditional irrigation communities in each geographical sector (Table 1). These data came from the Sierra Nevada Acequias Inventory (Cano-Manuel 2000, Fernández-Escalante et al. 2006) and the Andalusian Inventory and Characterization of Irrigated Lands (Table 1). Direct driver of change: land-use intensification The Spanish National Ecosystem Assessment identified land-use change as the most important direct driver of change within Spanish semi-arid systems (Spanish NEA 2014). In this study, we considered the impacts of a common land-use transition that has been experienced across many Spanish basins: land-use intensification. This land-use trend was quantified in each of the seven geographical sectors using the percentage of surface dedicated to greenhouses and urbanization (data from the Andalusian Multi-territorial Information System, see Table 1). Interactions between biophysical and socio-cultural factors in coupled SESS We used Spearman nonparametric correlation tests to determine the relationships between biophysical (i.e., hydrological and biological), ecosystem service (i.e., supply and social demand), local water governance, and land-use intensification factors ($n = 7$) across the seven geographical sectors previously identified in the Adra and Nacimiento watersheds. The correlations were mainly used to explore supply-supply associations by examining the influence of biophysical and local governance factors on the supply of the different ecosystem services. To visualize and compare the spatial patterns of the interactions that occurred among the factors, we standardized and then transformed all data to a common scale of 0-1, rescaling data to the maximum value observed in each sector. Finally, we created flower diagrams for the different geographical sectors in each watershed. The comparison of flower diagrams in different locations provides information on spatial supply-demand trade-offs based on biophysical, ecosystem service (supply and social demand), and local water governance factors in the different geographical sectors in the Adra and Nacimiento watersheds, taking into account the land-use intensification. For simplification, biological factors in flower diagrams refer to only the functional dispersion index of vegetation and macroinvertebrates (i.e., FDis veg, FDis macro). RESULTS Hydrological factors The pattern of blue (BWF) and green (GWF) freshwater generation follows a clear geographical gradient (maps are shown in Appendix 3). The greatest green freshwater (GWF) flows originate in the headwaters of both watersheds (sectors N1 and A1; Table 2) because these sectors receive the most rainfall and have the highest forest vegetation cover (Fig. 2). In the lower parts of the watersheds (sectors N4 and A3), rainfall and vegetation cover decrease, reducing the green freshwater (GWF). The flow of rainfall diverted to feed surface and groundwater bodies (blue freshwater flow, BWF) is also higher in the upper reaches of both watersheds (sectors N2 and A1). In total, 116 plant species from 40 families (the most prominent were Leguminosae, Fagaceae, Salicaceae, Labiatae, Compositae, and Gramineae) were observed across both watersheds. Although the highest values of species diversity were found in the high mountain (sector A1, H veg = 4.20), lower values were found in the lower Adra
(sector A3, H veg = 3.21) and Nacimiento watersheds (sector N3, H veg = 2.78; Table 2). We found the highest values of functional dispersion in sector A2 (FDis veg = 5.69) and lower values in sector N3 (FDis veg = 1.94, which also had lower diversity). Macroinvertebrates from 57 genera belonging to 9 orders (Rhynchobdellia, Basommatophora, Coleoptera, Diptera, Ephemeroptera, Veneroidea, Odonata, Plecoptera, and Trichoptera) were recorded. We found the highest diversity estimations of macroinvertebrates in sector N2 (H macro = 3.39), followed by sector A1 (H macro = 3.21, Table 2), where there was a predominance of Trichoptera, Ephemeroptera, and Coleoptera families. We did not find any macroinvertebrates in sectors N3, N4, and A3, corresponding to the most downstream areas in each watershed, which had ephemeral streams with no water during the sampling period. The same tendency was observed for functional dispersion (FDis macro); the highest values were found in sectors N2 and A1). Ecosystem services: supply and social demand The supply of the ecosystem services of freshwater (in terms of BWF), water quality (WQ), and erosion control (ERO) was higher in the upper reaches of both watersheds. The surface occupied by traditional crops followed the same gradient from upper to lower watershed in both basins, with the exception of sector A1, whose area is mainly located in the protected area. Thus, in the Adra watershed the geographical sector A2 involved the largest area of traditional agriculture (TA, 43.34% of the surface) together with N1 (22.53% of the surface); both sectors were also characterized by high green freshwater flows (GFW, Table 2) that maintain suitable soil moisture conditions for crops. Higher levels of ecotourism were related to the upper parts of the watersheds and the protected area. In general, the ecosystem services with a higher social demand (named by more than 20% of respondents) included traditional agriculture, air quality, and ecotourism in almost every geographical sector (Table 2). Clean energy was one of the most important services cited in all the Nacimiento sectors, where wind farms have increased considerably in the last 10 years. In the lower Adra (sector A3), freshwater and intensive greenhouse agriculture were the principal ecosystem services demanded. In addition and particularly evident in the Adra watershed, the ecosystem service demand was more diversified in the upstream areas (sector A1), becoming more restricted in downstream areas (sector A3). In relation to the selected ecosystem services, the demand for a particular service was higher in those sectors where the service was clearly provided or where the population would like to enjoy or use this service; this is a reflection of what respondents would like to obtain from the watershed. For example, the demand for traditional agriculture (TA) was important in those sectors traditionally associated with agricultural activities (sectors N1 or A2), and in N4, where the surface occupied by traditional crops is low but it could be a way to revitalize its population. Similarly, the social importance of erosion control (ERO) and water quality was high in those sectors with a better supply of these services (sectors N1 and A1) and in those sectors where these services are deteriorating, e.g., sector A3 (Table 2) and the number of traditional irrigation communities (Aceq 2), was found in sector A3 in the Adra watershed, because it corresponds to the lowest watershed sector in which acequias have been replaced by pipes for intensive agriculture. In the Nacimiento watershed the situation was similar across the different geographical sectors (Table 2). Direct drivers of change: land-use intensification Land-use intensification (INT) levels followed a particularly strong north-south gradient in the Adra watershed, with the upper parts of the watersheds being more intensified than upper parts. In fact, 12.27% of the surface is occupied by greenhouses or urbanization in sector A3 (Table 2). Interactions between biophysical and socio-cultural factors in coupled SESS Associations between biophysical and socio-cultural factors underpinning ecosystem services supply Spearman rank correlations indicated positive significant relationships between hydrological and local water governance factors (BWF-Aceq 1, BWF-Aceq 2) and between hydrological and biological factors (GWF-FDis veg; Fig. 3). Specifically, we found that blue freshwater flows (BWF) were strongly related to the conservation status of acequias (Aceq 1) and number of traditional irrigation communities (Aceq 2). Similarly, green freshwater flows (GWF) were positively related to the FDis veg. Regarding the interaction between biological factors and the supply of ecosystem services, our results showed a significant positive relation among the Shannon-Weaver diversity index of riparian vegetation (H veg), macroinvertebrates (H macro), the functional dispersion index of macroinvertebrates (FDis macro), and the supply of water quality (WQ) as a regulating service (Fig. 3). This association is consistent with the role of these biological communities in maintaining water quality (WQ). Likewise, we found positive correlations between the riparian vegetation (H veg), macroinvertebrates diversity (H macro), functional dispersion index of macroinvertebrates (FDis macro), and the ecotourism (ECOT) variable (Fig. 3). This indicates that suitable areas for ecotourism were associated with conserved natural environments. Examining the relationships among ecosystem service, we found a positive correlation between both regulating services, i.e., where erosion control (ERO) was higher, water quality (WQ) was also higher (Fig. 3). Likewise, ecotourism (ECOT) and erosion control (ERO) were positively correlated. The social importance of freshwater (FW) was correlated with the social importance of water quality (WQ), indicating that the social demand of both water-related services is located in the same geographical sectors (Fig. 3). Examining ecosystem service demand, a negative relation was observed between the importance of erosion control (ERO) and traditional agriculture (TA), indicating that in those geographical sectors where the demand for erosion control was higher there was less social importance specified for traditional agriculture. In contrast, the social demand for ecotourism (ECOT) was higher when blue freshwater flows (BWF) and local water governance factors were higher too (Aceq 1). It is also interesting to note that when local water governance (Aceq 1, Aceq 2) was higher, there was a lower social demand for regulating services (WQ, ERO; Fig. 3). Finally, land-use intensification (INT) was significantly negatively correlated with most of the biological factors (H macro, H veg, FDis macro) and with the supply of ecosystem services, particularly with ecotourism (Fig. 3). Spatial patterns of the interactions: supply-demand trade-offs Clear spatial trade-offs were found for the interactions among biophysical and socio-cultural factors, and among ecosystem services supply and social demand in both watersheds; this was particularly noticeable between the upper and the lower stream of the Adra watershed (Fig. 4). In addition, when biological factors were maintained (H veg, H macro, FDis macro), the supply of ecosystem services was also high, particularly the supply of water quality (WQ) and ecotourism (ECOT; Fig. 3). Ecological integrity in terms of the biophysical factors underpinning ecosystem services (i.e., BWF, GWF, FDis veg, FDis macro) and ecosystem services supply was maintained upstream (WQ, ERO, ECOT); however, in the downstream areas ecosystem service demand for freshwater (FW) and erosion control (ERO) was greater and freshwater consumption (FWC) was much higher (Fig. 4). Furthermore, downstream areas had higher land-use intensification (INT). Particularly in the Adra watershed, the geographical areas with higher levels of land-use intensification have lost the biophysical capacity to supply ecosystem services. However, they maintained a high level of freshwater consumption and social demand for ecosystem services, which were in fact degraded, especially traditional agriculture (TA), erosion control (ERO), and water quality (WQ; Fig. 4). The overall patterns of the Nacimiento watershed followed a west-east gradient with a lower effect of land-use intensification (INT) across geographical sectors. All sectors were affected in a similar way (except sector N3, Fig. 4) because intensive agriculture is located in the valley bottoms of the mountains bordering the watershed. In the Nacimiento watershed one of the principal limitations is the groundwater resources. Freshwater flows (BWF, GWF) along the watershed decrease, with a parallel reduction in ecosystem service supply, particularly traditional agriculture (TA), water quality (WQ), and erosion control (ERO; Table 2, Fig. 4). Furthermore, users across sectors follow different strategies in terms of their ecosystem service demand. Sectors N2 and N3 were more focused on services related to the tertiary sector such as ecotourism, whereas N1 and N4 were interested in ecotourism (ECOT), but especially in traditional agriculture (TA; Table 2, Fig. 4), even when the biophysical factors were not favorable (e.g., sector N4 had the lowest freshwater flows in Nacimiento watershed). DISCUSSION Quijas et al. (2012) highlight that plant diversity and water availability represent the key biotic and abiotic factors, underpinning the supply of ecosystem services. This statement is supported by our findings, which show that the maintenance of both blue and green freshwater flows, and biological (riparian vegetation and aquatic macroinvertebrates) trait-based indicators are essential for providing a diverse flow of ecosystem services and maintaining sustainable SESS in this semi-arid system (see Fig. 4). A spatial pattern of biophysical and
socio-cultural interactions was found to occur along the watersheds (from the upper to the lower watershed), resulting in spatial trade-offs of ecosystem services in relation to different levels of land-use intensification, biophysical conditions, and water governance. Increasing the understanding of the functional consequences of drivers of change on biodiversity is critical for guaranteeing the supply of ecosystem services. Our results showed an association between more intensified areas and lower vegetation diversity; however, a clear association between land-use intensification and the functional dispersion index of vegetation was not apparent (see Fig. 3). This is supported by Laliberté et al. (2010), who observed that land-use intensification impacts on the functional attributes of plant communities and, consequently, increases vulnerability to future disturbances. The use of trait-based indicators has been recommended in recent studies to predict the effect of different factors on ecosystem service supply (Lavorel 2013) and also to provide biodiversity information that is comparable across regions, unlike taxonomic indicators, i.e., composition of communities, that are conditioned to particular areas. However, trait-based indicators do not take into account particular species that could be the objective of conservation programs, such as threatened and endemic species (Vandewalle et al. 2010). In addition, current information on explicit associations between traits and ecosystem services is still not well documented for many taxonomic groups (Lavorel 2013). Thus, there is a need to use complementary approaches, such as species diversity metrics (Vandewalle et al. 2010). In this study, the selected biological factors were based on traditional diversity metrics (Shannon-Weaver index) and trait-based indicators of riparian vegetation and aquatic macroinvertebrates. Intensive agriculture has been shown to disturb the ecological integrity of wetlands in semi-arid Spain (Ortega et al. 2004). More intensified parts of our study areas, particularly in the low Adra, sector A3, were characterized by the lowest values for hydrological and biological factors (Fig. 4). In the lower Adra (sector A3), intensive horticulture experienced a boom beginning in the 1970s (Sánchez-Piçón et al. 2011). Within the last few decades, the area devoted to horticulture has increased from 3000 ha in 1975 to 27,000 ha in 2008, making Almería the Spanish province with the largest area of greenhouses in the Mediterranean basin (Aznar-Sánchez et al. 2011). As expected, increased water demand has been essential for this agricultural intensification (Downward and Taylor 2007, Quintas-Soriano et al. 2014), and as shown in our findings, sector A3 had the highest percentage of respondents demanding freshwater and water quality, and also the highest figures for water consumption (Table 2). In this sense, the Adra watershed could be seen as a classical spatial trade-off example, in which upstream users maintain the ecological integrity while downstream users demand ecosystem services (Maass et al. 2005, Palomo et al. 2013). According to our results, biological and hydrological factors were higher in the upper areas of the watershed, whereas the pressures and the ecosystem service demand were more intense in lower areas (Fig. 4). This spatial mismatch in pattern is related to an ecosystem service trade-off management decision that provisioning services are preferred, prioritizing the short-term needs of society (Rodríguez et al. 2006). Similar results were found by Butler et al. (2013), who observed that different land-use management options generated trade-offs between promoting food production and water quality regulation in an Australian catchment. Land-use change motivated by economic gains and market services, such as intensive agriculture, also needs to consider the diversity of other ecosystem services and their associated values (Bateman et al. 2013). Changing the focus of agricultural management from the maximization of food production to the production of food combined with other ecosystem services could help increase social-ecological resilience (Gordon et al. 2010) and the viability of rural areas through the diversification of the services provided (Power 2010, Di Iacovo et al. 2014). We found that land-use intensification, focused on the overexploitation of one unique provisioning ecosystem service (intensive agriculture), has increased the economic growth in the region (Aznar-Sánchez et al. 2011). However, it has also resulted in (1) losses of the biophysical factors responsible for the supply of other ecosystem services, (2) the social demand for ecosystem services becoming more intensive and less diversified, and (3) the abandonment of traditional and local governance practices that influence social capital and the maintenance of other ecosystem services. In the Nacimiento watershed, land-use intensification had a lower impact on ecosystem service trade-offs because it does not follow the classical upstream-downstream model; all sectors are similarly affected by intensive agriculture. The main drivers of change are demographic (aging and depopulation), gender change (masculinizing their populations), and land-use abandonment (Niesta-Arandia et al. 2014). As mentioned, this watershed suffers from water supply limitations downstream because of its semi-arid status and erosion problems related to the mountain topography. In this watershed, the traditional agriculture practices of terraces and acequias have facilitated the preservation of biophysical components (water flows and biological traits) upstream and, thereby, the supply of ecosystem services. On the contrary, in the eastern part of the watershed, the supply of ecosystem services is low and the social demand of traditional agriculture downstream is high (Fig. 4). These results show the relevant role of traditional practices in agriculture to promote soil and water conservation through the use of terraces and acequias, respectively (Niesta-Arandia et al. 2015). The viability of this area therefore requires the maintenance of traditional agricultural practices that are adapted to the extreme semi-arid conditions. In terms of local governance practices, acequias do not function merely as water canals (Archambault and Ullibari 2007). As Niesta-Arandia et al. (2015) described, water infiltration in acequias contributes to the maintenance of broad leaf vegetation species and humid habitats for other species (Espin et al. 2010), promoting regulating services, such as microclimatic regulation and water-related ecosystem services (Pulido-Bosch and Ben Shih 1995). In addition, local irrigation communities promote the maintenance of local practices and social capital (Rodríguez 2006, Waylen et al. 2010). However, this traditional system is threatened by two principal indirect drivers: (1) rural abandonment caused by depopulation and the conversion of the economy to the service sector (Pineda 2001) and (2) the intensification of agricultural systems, including the introduction of modern irrigation canals (Spalding 2000, Niesta-Arandia et al. 2015). If the acequia system falls into disuse, the terraced agricultural system will suffer the same consequence, resulting in increased soil erosion (Douglas et al. 1994) or degradation of the stability of a particular terrace-acequia-vegetation system (Spalding 2000). The current situation, in which this traditional irrigation system is advocated to be abandoned or modernized, could compromise the SESS' sustainability, i.e., the capacity to provide a diverse flow of ecosystem services to satisfy human needs while maintaining the management strategies and ecological processes underpinning services. It is now acknowledged that in the Mediterranean, ecosystems have been sustained through a complex historical relationship between SES subsystems, where socio-cultural capital and traditional practices play an important role in natural capital conservation and the maintenance of a diverse flow of ecosystem services (Martín-López et al. 2012). In the Mediterranean region, ecosystems with differing degrees of extensive human management provide a greater diversity of ecosystem services compared with either pristine or intensified ecosystems (Bugalho et al. 2011, Willaarts et al. 2012). In this study, the geographical sectors (N2, A1, A2) with higher values for biophysical and local water governance factors were also characterized by diverse and lower social demands for ecosystem services (Fig. 3). Our results suggest that ecosystem service trade-offs are determined by the joint operation of biophysical and socio-cultural factors (Fig. 4) and, in turn, demonstrate that ecosystem services are coproduced by both ecosystems and social systems (Reyers et al. 2013). Similarly, the Intergovernmental Platform on Biodiversity and Ecosystem Services has recently recognized in its conceptual framework that ecosystem services are coproduced by nature and anthropogenic assets, i.e., biophysical and socio-cultural factors, respectively (Diaz et al. 2015). Consequently, any attempt to manage SESS toward sustainability should identify the key functional factors (both biophysical and socio-cultural) that are essential for maintaining ecosystem service supply. However, the majority of studies on ecosystem service trade-offs only focus on associations between ecosystem services (Bennett et al. 2009). In this study, we take a step forward by assessing trade-offs between ecosystem services and between the factors that generate, or may influence, the supply and demand of ecosystem services, as well as their trade-offs. However, the analysis of associations between biophysical and socio-cultural factors, and between these factors and supply-supply and supply-demand trade-offs, entails high levels of complexity. Biophysical factors are usually measured in ecological units,
whereas socio-cultural factors refer to administrative boundaries (Raudsepp-Hearne et al. 2010). This research used homogeneous geographical sectors and economic, demographic, social, resource-use, and land-use variables (for more details, see Niesta-Arandia et al. 2011). Although the reduction of social-ecological complexity to homogeneous geographical sectors implies some loss in detailed information and data availability (and therefore limits to data analysis), it also facilitates spatial comparisons of interlinked components within SESS. The management of SESS should consider ecosystem service trade-offs, as well as the biophysical and socio-cultural factors responsible for these trade-offs, to generate useful and suitable information for environmental planning and decision making. This study provides a quantitative analysis of the biophysical and socio-cultural factors underlying ecosystem service interactions through correlations to test linear associations (but not causalities) and the construction of flower diagrams to visualize spatial patterns. It also explores how these methods can provide the basis for studying trade-offs. Further research challenges include understanding trade-offs within a temporal context to compare temporal trends, application of additional methods to better examine spatially explicit variations, and the exploration of causalities between different management strategies and ecosystem service supply (Mouchet et al. 2014). Although there are several scientific challenges in ecosystem service trade-off research, conceptually this study advances knowledge through the demonstration of those biophysical and socio-cultural factors that coproduce and determine ecosystem services in semi-arid SESS (Fig. 1). Finally, our findings highlight the necessity of conducting social-ecological, place-based research for acquiring a comprehensive understanding of complex inter-relationships within SESS that result in ecosystem service trade-offs. ACKNOWLEDGMENTS The authors gratefully acknowledge the Sierra Nevada National and Natural Park staff and the Department of Environment of the Andalusian Government staff for providing the facilities to obtain data. We really appreciate the valuable comments made by S. Diaz and D. Cáceres on the first steps of the research. We thank I. Palomo for the cartographic work. We are grateful for the detailed comments provided by two anonymous reviewers. 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