Contributed Paper

Use of demand for and spatial flow of ecosystem services to identify priority areas

Willem Verhagen,[1]* Aija S. Kukkala,[2] Atte Moilanen,[3] Astrid J.A. van Teeffelen,[1] and Peter H. Verburg[1]

[1]Environmental Geography Group, Department of Earth Sciences, Faculty of Earth and Life Sciences, Vrije Universiteit Amsterdam, De Boelelaan 1085, 1081HV Amsterdam, The Netherlands
[2]Department of Geosciences and Geography, University of Helsinki, P.O. Box 68, FIN-00014 Helsinki, Finland
[3]Finnish Centre of Excellence on Metapopulation Biology, Department of Biosciences, Biocenter 3, University of Helsinki, P.O. Box 65 (Viikinkaari 1), FI-00014 Helsinki, Finland

Abstract: *Policies and research increasingly focus on the protection of ecosystem services (ESs) through priority-area conservation. Priority areas for ESs should be identified based on ES capacity and ES demand and account for the connections between areas of ES capacity and demand (flow) resulting in areas of unique demand–supply connections (flow zones). We tested ways to account for ES demand and flow zones to identify priority areas in the European Union. We mapped the capacity and demand of a global (carbon sequestration), a regional (flood regulation), and 3 local ESs (air quality, pollination, and urban leisure). We used Zonation software to identify priority areas for ESs based on 6 tests: with and without accounting for ES demand and 4 tests that accounted for the effect of ES flow zone. There was only 37.1% overlap between the 25% of priority areas that encompassed the most ESs with and without accounting for ES demand. The level of ESs maintained in the priority areas increased from 23.2% to 57.9% after accounting for ES demand, especially for ESs with a small flow zone. Accounting for flow zone had a small effect on the location of priority areas and level of ESs maintained but resulted in fewer flow zones without ES maintained relative to ignoring flow zones. Accounting for demand and flow zones enhanced representation and distribution of ESs with local to regional flow zones without large trade-offs relative to the global ES. We found that ignoring ES demand led to the identification of priority areas in remote regions where benefits from ES capacity to society were small. Incorporating ESs in conservation planning should therefore always account for ES demand to identify an effective priority network for ESs.*

Keywords: ecosystem-service flows, European Union, land targets, spatial prioritization, systematic conservation planning, Zonation software

Uso de la Demanda y el Flujo Espacial de los Servicios Ambientales para Identificar Áreas Prioritarias

Resumen: *Las políticas y las investigaciones cada vez más se enfocan en la protección de los servicios ambientales (SAs) por medio de la conservación de áreas prioritarias. Las áreas prioritarias para los SAs deberían ser identificadas con base en la capacidad de SAs y la demanda de SAs, y deberían representar las conexiones entre las áreas de capacidad de SAs y la demanda (flujo), resultando así en áreas de conexiones únicas de demanda y suministro (zonas de flujo). Probamos maneras para representar la demanda de SAs y las zonas de flujo para identificar las áreas prioritarias en la Unión Europea. Mapeamos la capacidad y la demanda de un SA global (secuestro de carbono), regional (regulación de inundación), y tres locales (calidad del aire, polinización, y tiempo libre urbano). Usamos el software Zonation para identificar las áreas prioritarias para los SAs con base en seis experimentos: con y sin representación de la demanda de los SAs, y cuatro experimentos que representaron el efecto de la zona de flujo de los SAs. Sólo hubo un traslape de 37.1 % entre el 25 % de las áreas prioritarias que englobaron la mayoría de los SAs con y sin representación de la demanda de SAs. El nivel de los SAs que se mantuvo en las áreas prioritarias incrementó de un 23.2 % a 57.9 % después de considerar la demanda de los SAs, especialmente para aquellos SAs con una zona de flujo*

*email *willem.verhagen@vu.nl*
Paper submitted May 17, 2016; revised manuscript accepted November 27, 2016.

Conservation Biology, Volume 31, No. 4, 860–871

DOI: 10.1111/cobi.12872

reducida. Representar la zona de flujo tuvo un pequeño efecto sobre la ubicación de las áreas prioritarias y el nivel de SAs que se mantuvo, pero resultó en menos zonas de flujo sin SAs mantenidos en relación a ignorar las zonas de flujo. Representar la demanda y las zonas de flujo mejoró la representación y distribución de los SAs con zonas de flujo de regionales a locales sin compensaciones grandes en relación al SA global. Hallamos que ignorar la demanda de SAs llevó a la identificación de las áreas prioritarias en las regiones remotas en donde los beneficios de la capacidad de los SAs para la sociedad fueron pequeños. Incorporar los SAs a la planeación de la conservación por lo tanto debería siempre representar a la demanda de los SAs para identificar una red efectiva de prioridades para los SAs.

Palabras Clave: flujos de servicios ambientales, objetivos terrestres, planeación sistemática de la conservación, priorización espacial, software Zonation, Unión Europea

Introduction

Conservation planning increasingly incorporates ecosystem services (ESs) alongside biodiversity (Luck et al. 2012; Cimon-Morin et al. 2013). Conservation planning for ESs is often implemented through land-management targets, including Aichi target 11, which aims to conserve 17% of the land for biodiversity and ESs (Convention on Biological Diversity 2010). Because land is scarce and funding is limited it is necessary to identify an efficient and effective network of priority areas for ESs. Spatial conservation prioritization provides the tools to do so (Moilanen et al. 2009). Although developed for identifying biodiversity priority areas the approach has also been used for ES prioritization (Chan et al. 2006; Casalegno et al. 2014; Cimon-Morin et al. 2014; Schröter et al. 2014). There are, however, differences between prioritizing areas for ESs and prioritizing areas for biodiversity (Luck et al. 2012). Ecosystem services are the benefits humans obtain from nature (MEA 2005). Ecosystem functions and processes only become ESs when there is a demand for the service (Fisher et al. 2009). In setting priority areas for ESs, one needs to account not only for the capacity of an ecosystem to provide a service but also for spatial variation in ES demand (Wolff et al. 2015). Studies on ES prioritization need to directly link demand and supply at a location.

However, areas with high ES capacity and the location of human beneficiaries do not necessarily coincide. The spatial connections between areas of ES capacity and areas of ES demand are called ES flow (Fisher et al. 2009). ES flow links areas of ES capacity and demand and ranges from global to local. Habitat for pollinators needs to be protected close to croplands, whereas forests sequestering carbon can be conserved anywhere. For each ES, it is possible to identify the flow zone, the area over which ES capacity and demand can be spatially linked. Priority areas for ES, therefore, need to be distributed across flow zones in order to be effective. Identifying priority areas for ESs thus needs to account for the spatial variation in ES demand and the ES flow zone.

Studies on prioritization of ESs do not always account for the spatial variation in ES demand. Cimon-Morin et al. (2014) found large differences between priority areas identified with and without accounting for demand. However, in their study, areas of ES demand and ES capacity did not have to overlap, meaning priority areas could have high ES demand and low ES capacity or vice versa.

Few researchers have accounted for the flow zone of ESs. Orsi et al. (2011) assessed wood production by incorporating travel distance between communities and forests, and Chan et al. (2006) accounted for flow zones by assigning flood-protection targets per catchment or recreation targets per city. To our knowledge, no one has quantitatively assessed approaches for ES prioritization combining ES demand and the distribution of ES.

We sought to quantify the importance of accounting for demand and flow zones of ESs in identifying priority areas. Specifically we asked, how is the spatial allocation of priority areas for ESs and the level of ESs contained within top-priority areas affected by accounting for the level of ES demand and for the flow zone of individual ESs? We used the European Union (EU) as study area to address these questions. European Union policies are developed to protect and enhance ESs, such as the EU Biodiversity Strategy 2020 and the Strategy on Green Infrastructure (European Commission 2011, 2013). The EU biodiversity strategy aims to halt the loss of ESs, but actions toward this have mostly focused on ES capacity without accounting for the actual use or demand for ESs (Maes et al. 2016). Testing the effect of consideration of demand for ESs and flow zones in identifying areas of conservation priority is relevant to the effective implementation of these types of policies.

Methods

We used four regulating and one cultural ES for which both ES capacity and demand maps were available for the EU at a 1-km resolution (Table 1). The ESs encompassed global (carbon), regional (flood control), and local (pollination, air quality, and urban leisure) ES flows. We included carbon sequestration as an example of a global-flow ES to test whether focusing on more localized ESs resulted in declines in carbon sequestration. We mapped

Table 1. Summary of the ecosystem services and their flow zones used.

Ecosystem service	*Source*	*Spatial flow*	*Flow zone*	*No. of flow zones*	*Median flow-zone area, range (km²)*
Air quality	Maes et al. 2015	local	EU city and commuting zone	436	773, 11–17470
Carbon sequestration	Schulp et al. 2008	global	EU	1	NA
Flood regulation	Stürck et al. 2014	regional	subcatchments >2 km²	3878	250, 2–21574
Pollination	Schulp et al. 2014	local	10×10 km area	37194	100, 100-100
Urban leisure	supporting information	local	EU city plus 8 km buffer zone	538	767, 302–5363

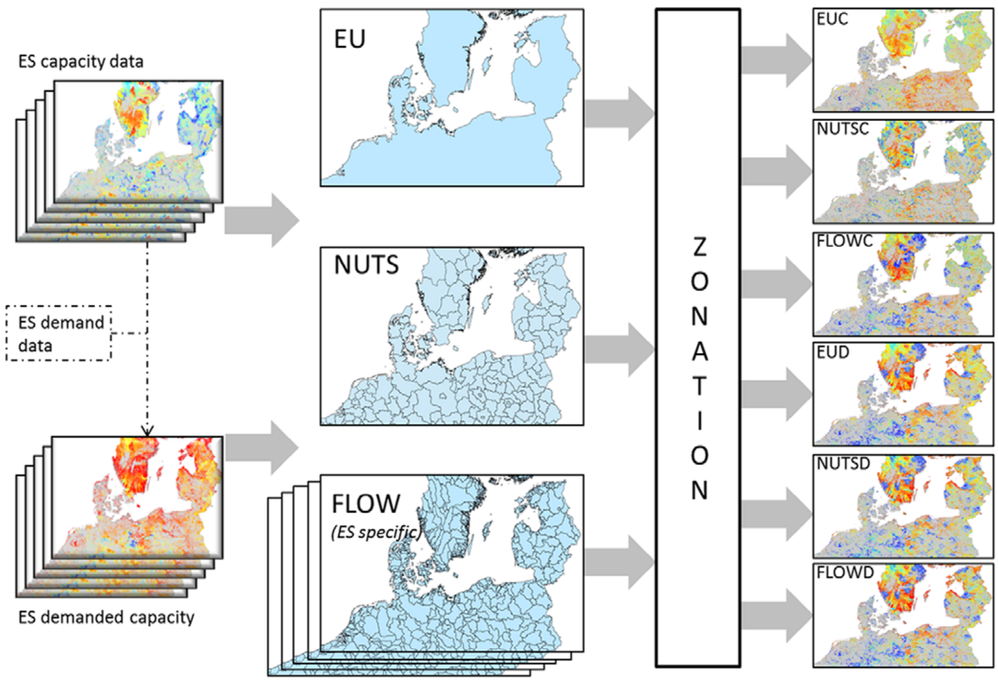

Figure 1. Schematic overview of the setup of our priorization of ecosystem services (ESs). Two sets of ES input maps are split into 3 different sets of spatial delineations. This results in a single map per ES for the EU, per NUTS (EU administrative unit), or per flow zone (an area with a unique demand–supply combination dependent on the ES flow) used as an input to the prioritization analysis. The 6 tests (EUC, NUTSC, FLOWC, EUD, NUTSD, and FLOWD) are described in Methods. Examples of priority areas are depicted on the left and right maps where red is low priority and blue is high priority.

the landscape's capacity to provide ESs (ES capacity) and the portion of ES capacity demanded by society, derived by combining ES demand and ES capacity maps. We used ES capacity and ES capacity-demanded data as inputs in our prioritization analyses (Fig. 1). To test the effect of accounting for flow zones, we used either a single map per ES (EU), a map of ESs by administrative unit (NUTS [an EU administrative unit]), or a map per ES flow zone (FLOW) in the prioritization analyses (Fig. 1).

ES Data and Flow Zones

Carbon sequestration capacity maps were derived from Schulp et al. (2008), who used a bookkeeping approach combining belowground carbon sequestration for all land-cover types with aboveground carbon sequestration in forests (teragram C per year). We used the carbon sequestration map for 2000 and set negative carbon sequestration values to zero. Because fulfilling the demand for carbon sequestration is not spatially constrained, we considered carbon sequestration a global-flow ES. Hence, carbon-sequestration capacity demanded was set equal to ES capacity. The flow zone of carbon sequestration was the entire EU.

Flood-regulation capacity and demand maps were derived from Stürck et al. (2014), who assessed flood-regulation capacity based on land cover, catchment type, precipitation, catchment zone, water-holding capacity, land use, and land management. Catchments were delineated using a European catchment map (EEA 2008), where catchments were delineated based on a digital elevation model, landscape stratification, and coastline data. The resulting catchments are Strahler order-5 catchments, often representing subcatchments. We used potential flood damage, calculated using the damage-scanner model of Bubeck et al. (2011) as a proxy for flood-regulation demand. Damage was calculated using land-cover-specific damage curves (€/ha) for a 50-year flood-inundation level. Damages were aggregated per subcatchment. Then, the aggregated downstream demand for flood regulation per subcatchment was divided by the area of the upstream subcatchments that could provide flood regulation (Stürck et al. 2014). This approach accounted for all benefits downstream of a subcatchment. Values of flood-regulation demand were normalized from 0 to 1. We calculated the portion of the flood-regulation capacity demanded by multiplying the ES capacity per cell by the normalized ES demand per catchment. For flow tests (Fig. 1), we used subcatchments, which resulted in 3,878 flow zones (Table 1).

Air-quality-regulation capacity and demand maps were derived from Maes et al. (2015) for NO_2 emissions. Air-quality capacity was quantified using deposition velocity (m/s), mainly determined by the leaf area of plants (Derkzen et al. 2015). Emissions of NO_2 originate from transport and industry fuel combustion. We used modeled NO_2 concentrations (micrograms per cubic meter) as a proxy for air-quality-regulation demand, assuming demand is high in locations with relatively higher air pollution (Pistocchi et al. 2011). Deposition velocity and concentrations of NO_2 were transformed to the same units (tons per square kilometer per year). We calculated the portion of air-quality capacity demand by multiplying the concentrations of NO_2 and deposition velocity for each cell. For flow tests (Fig. 1), we used cities' functional urban area delineations (GISCO 2011), which includes the urban area and its commuting zone, which resulted in 436 flow zones.

Pollination capacity and demand maps were derived from Schulp et al. (2014). Pollination capacity was mapped using potential wild-bee habitat per cell, assessed based on a reclassification of land-cover and hedgerow density. Pollination demand was a combination of the pollination dependency of a crop type (0–100%) and the share of that crop type within a 1-km^2 cell. We reassigned demand for pollination to cells with natural vegetation directly adjacent to croplands with the Moore neighborhood (i.e., 8 neighboring cells). We normalized data on pollination demand to values from 0 to 1 and combined it with pollination capacity. The flow zone for pollination is limited by pollinator flight distance. Most farmers have some opportunity to redistribute crops between fields and, thus, to redistribute benefits from pollination within a larger area. Redistribution of crops is likely to remain local, but no information exists on the extent to which farmers can redistribute crops. For flow tests (Fig. 1), we used a 10×10 km zone for pollination, assuming farmers have some opportunity to redistribute crops within this area. Only zones containing pollination-dependent crops were included, which resulted in 37,194 flow zones.

Urban leisure opportunities were mapped using a combination of land-cover data, distance to coasts, forest location characteristics, and agricultural landscape structure (see Supporting Information). We used population density in urban areas as a proxy for demand. Following Paracchini et al. (2014), for each cell we calculated the aggregated urban population density within an 8-km radius. We normalized data on population density to values from 0 to 1 and multiplied these values by ES capacity. Population-density data were skewed; some cells had very high population values. Therefore, we Winsorized the demand values based on the 95th percentile; that is, we assigned the 95th percentile value to all locations with values higher than the 95th percentile. For flow tests (Fig. 1), we delineated an 8-km buffer around European cities, which resulted in 538 flow zones.

Prioritization Approach

We prioritized areas with natural vegetation for ESs in the EU, thus excluding urban and water land-cover classes. Agricultural land was also excluded, except when hedgerows were present (van der Zanden et al. 2013). Croatia, Cyprus, and Malta were excluded because not all ES maps covered these countries.

We used the Zonation spatial prioritization software version 4 to identify priority areas (Moilanen et al. 2005, 2014; Lehtomäki & Moilanen 2013). Zonation was previously applied to identify priority areas for biodiversity (Pouzols et al. 2014) and ESs (Casalegno et al. 2014; Durán et al. 2014). Zonation produces a hierarchical prioritization of the entire landscape for multiple features (here ESs) simultaneously, based on weights and local occurrence levels of features, by iteratively ranking spatial units (here grid cells) to minimize aggregate loss of conservation value across features at each step (Lehtomäki & Moilanen 2013). It is important that a balance between features be maintained over the prioritization (Moilanen et al. 2014).

When applying Zonation, one needs to choose how Zonation aggregates value over many partially conflicting feature layers (a.k.a. the cell-removal rule). We used the additive-benefit function (ABF), which sums the loss of value across features converted via feature-specific benefit functions. The ABF is used to calculate value based on all features co-occurring at a location and thus gives comparatively high priority to areas that can cost-effectively cover features simultaneously (Moilanen et al. 2014).

We developed 6 tests that differed in how they accounted for ES demand and flow zones. Priority areas were identified based on ES capacity (ESC) without flow zones (EUC); ESC with uniform flow zones for all services in NUTS (NUTSC); ESC with a specific flow zone per service (FLOWC); ES capacity demanded (ESCD) without flow zones (EUD); ESCD with uniform flow zones for all services in NUTS (NUTSD); and ESCD with specific flow zones (FLOWD). Use of flow zones is consistent with the way Zonation prioritizes locations. Zonation operates by first selecting the entire landscape and then iteratively removing cells that contribute least to the total value of the solution (Moilanen et al. 2014). After each cell removal, Zonation updates the remaining cell values, accounting for what has been lost and what remains. We used EU-wide ES distributions in the EUC and EUD tests; thus, for example, the value of an ES supplied to city A increases when a cell supplying the same ES to city B is removed. In contrast, when accounting for flow zones, EU-wide distribution of ESs is broken into many independent flow zones (treated as independent features) and representation of ESs in one flow zone cannot be replaced by representation in another.

For the NUTS tests, we used EU NUTS regions as the flow zones of all ESs. For Belgium, Germany, and the Netherlands, we used NUTS2 regions. For the other member states, we used NUTS3 regions (Van Berkel & Verburg 2011). These NUTS regions consisted of aggregates of 1 × 1 km cells and ranged in area from 12.8 to 105869 km^2 (median 3614 km^2). We used ES capacity and capacity-demanded maps, respectively, for the NUTSC, and NUTSD tests. For the flow tests, we explicitly incorporated ES-specific flow zones and used ES capacity (FLOWC) and ES demanded-capacity (FLOWD) maps. With this approach, we aimed to maintain all ESs distributed across flow zones by accounting for the flow characteristics of each ES. Zonation settings are in Supporting Information.

Comparisons of Tests

We compared prioritization tests in 3 ways. First, we assessed the effect of accounting for demand by comparing the location of priority areas and the level of ES demanded capacity maintained (EUC vs. EUD). Second, we tested the effect of accounting for flow zone by comparing the location of priority areas and the level of ES demanded capacity maintained in the NUTS and FLOW tests. Finally, we tested whether accounting only for the ES flow zone (FLOWC & NUTSC) can be used as a proxy for ES demand. Demand maps for many ESs are nonexistent at the European scale (Maes et al. 2016), whereas ES capacity maps for many ESs are available, which makes such a simplification attractive.

We compared the degree of overlap in priority areas between tests. The overlap between tests was calculated for the top 1%, 2%, 5%, 10%, 17%, and 25% of the cells ranked as conservation-priority areas by calculating the percentage of identical cells in both sets. The 17% area corresponds to the global Aichi target for protected areas. Most results are presented for the top 17%. The level of ESs maintained, always calculated as the percentage of ES capacity maintained, within the priority areas was calculated at EU and flow-zone levels. At the EU level, we calculated the level of ES maintained with an increasing percentage of land retained as conservation-priority areas. To assess the level of ESs maintained per flow zone, we used 2 metrics. First, we calculated the percentage of prioritized cells within and outside a flow zone. Priority areas outside flow zones do not have an ES demand. Second, we calculated the percentage of ESs maintained per flow zone within the priority areas. Accounting for flow zones should result in a more even distribution of priority areas over flow zones.

Results

Accounting for ES Demand

Accounting for ES demand resulted in a clear shift in priority areas in the EU (Fig. 2). Priority areas for ES capacity (EUC) were located in remote areas such as northern Fennoscandia, western Scotland, and the Carpathians, as well as the Iberian Peninsula. Accounting for ES demand (EUD) shifted priority areas toward central European countries and natural vegetation in the proximity of cities, which was visually apparent for Sweden, Finland, and Scotland (Fig. 2). The overlap in priority areas between tests was low. For the top 1% of priority areas, 7.44% were identical, and for the top 25% of areas 37.1% were identical (Supporting Information).

Accounting for ES demand increased the level of ESs maintained in priority areas (EUC vs. EUD) (Fig. 3). For all ESs except carbon sequestration, the level of ESs maintained was large after accounting for demand. In part this result was expected because we measured ESs maintained as the demanded capacity maintained, but the increase in ES maintained after accounting for demand (EUC 23.2% vs. EUD 57.9%) indicated that priority areas based on ES capacity were in areas with no to low demand. The individual ESs were affected differently when accounting for ES demand, but local flow of ESs was most affected. The EUC test did not capture much of the demanded capacity of local-flow ESs (pollination 25.6%), whereas the demand tests captured large fractions (pollination 78.9%–80.8%) of the demanded capacity in a small fraction of the land. Accounting for demand and flow zone came with a efficiency loss for carbon sequestration (EUD 28.4% vs. FLOWD 28.0%), but the loss was relatively small compared with the gains for other ESs. In other words, there was no trade-off between global and regional or local ESs when accounting for demand.

The performance of the EUC test was especially poor for the local flow ESs because these ESs were very location specific. Air-quality regulation was provided only near emission sources. Because prioritization based

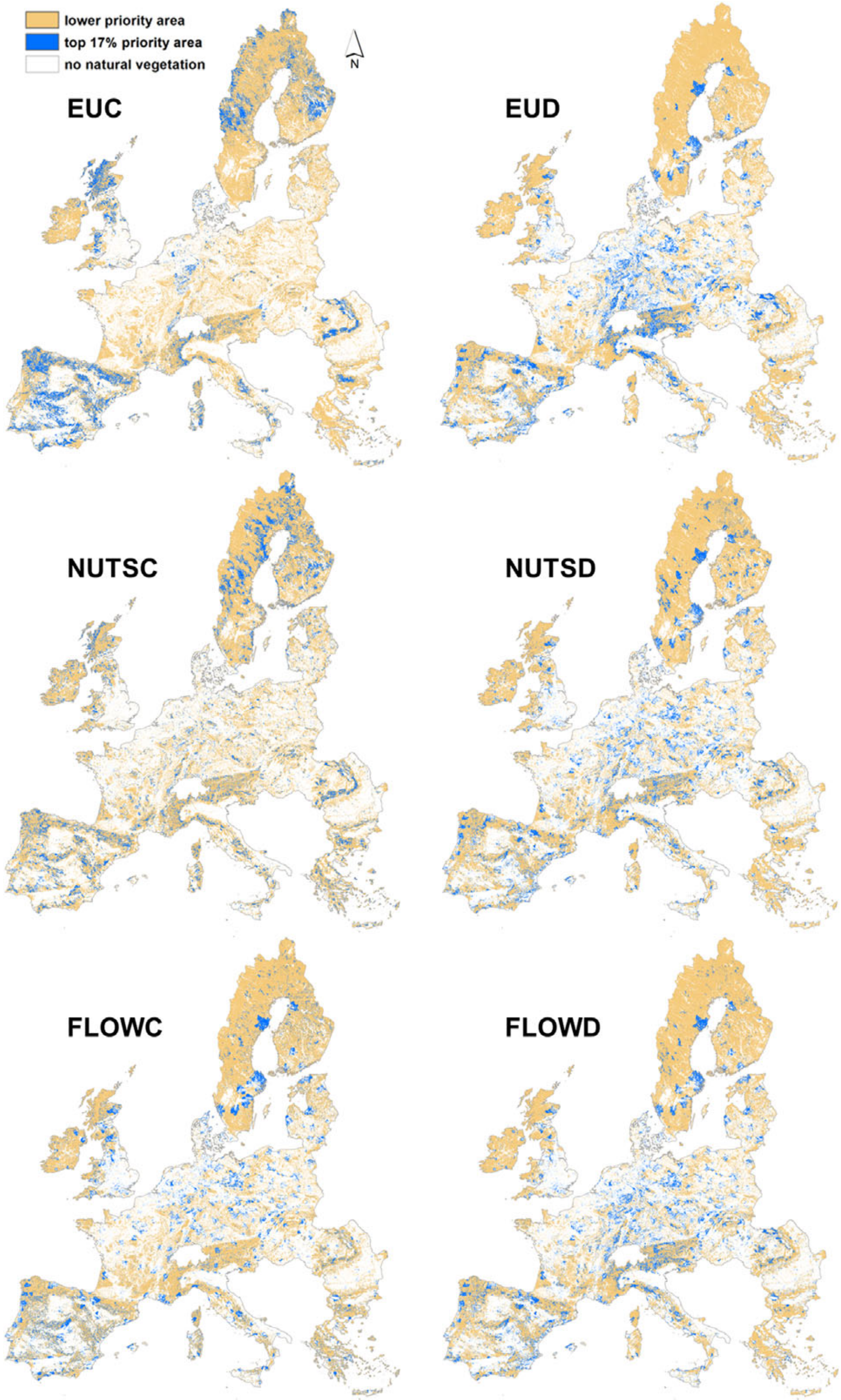

Figure 2. Location of 17% of priority areas that maintain the highest level of ecosystem services (ESs) in the EU based on 6 tests related to ES capacity, ES capacity demanded, and ES flow zone (an area with a unique demand-supply combination dependent on the ES flow). Tests are defined in Methods. Only areas containing natural vegetation were considered in the prioritization analysis. Croatia, Malta, and Cyprus are excluded because only partial information on ESs was available for these countries. The percent overlap between priority areas per experiment is in Supporting Information.

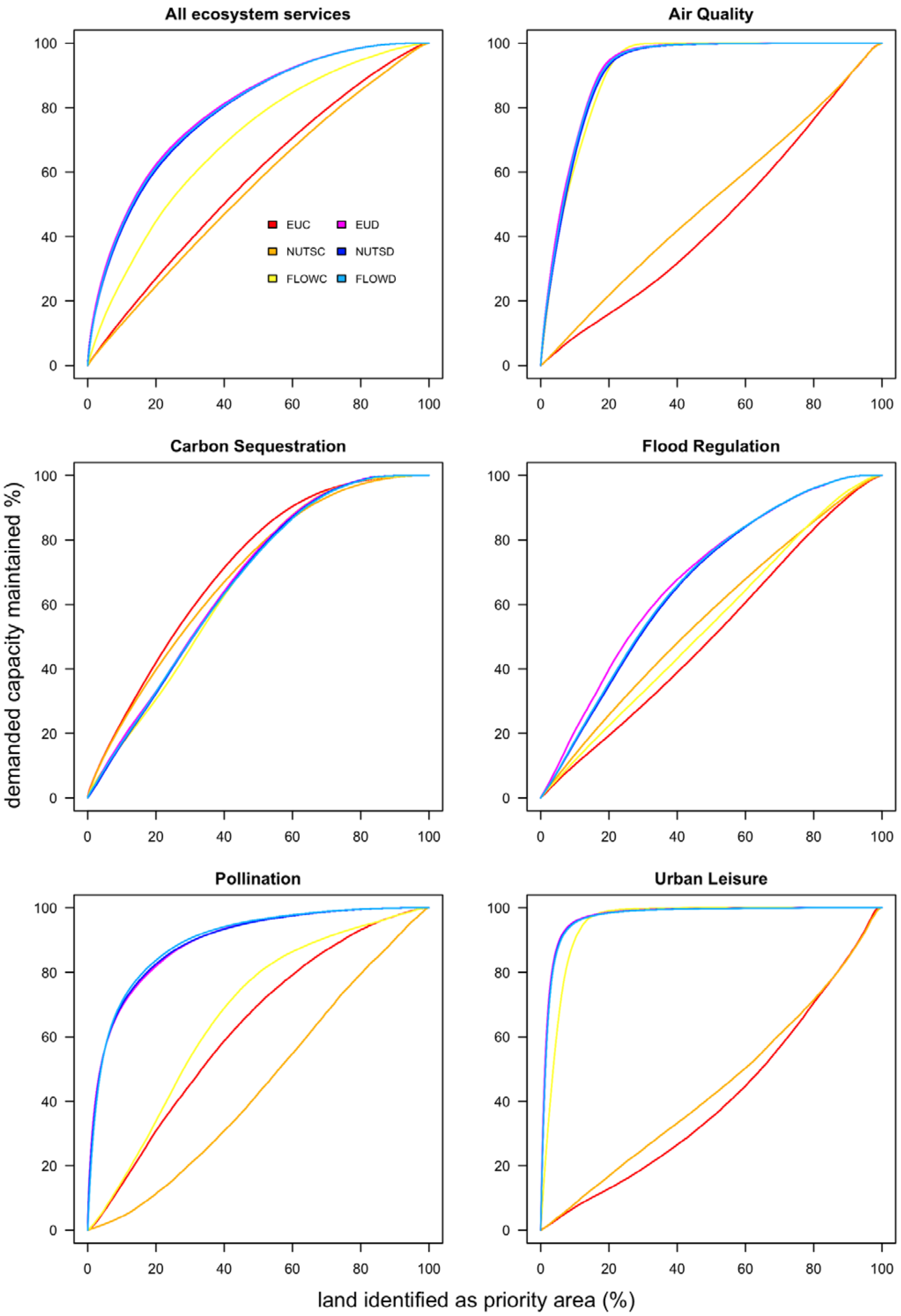

Figure 3. The level of ecosystem services (ESs) maintained (percent capacity demanded) in the EU relative to the percentage of conservation-priority areas identified based on 6 tests of ecosystem services capacity, demand, and flow zone (an area with a unique demand–supply combination dependent on the ES flow). Different degrees of concavity in the curves result from different size distributions of ESs across the landscape and from the fact that all prioritizations are based on the distribution of five ESs but results are presented per service.

on ES capacity did not consider that only ecosystems close to emission sources contribute to fulfilling ES demand, identified priority areas were often outside actual flow zones. For air quality, the EUC test allocated 90% of the top 17% of priority areas outside flow zones (Fig. 4).

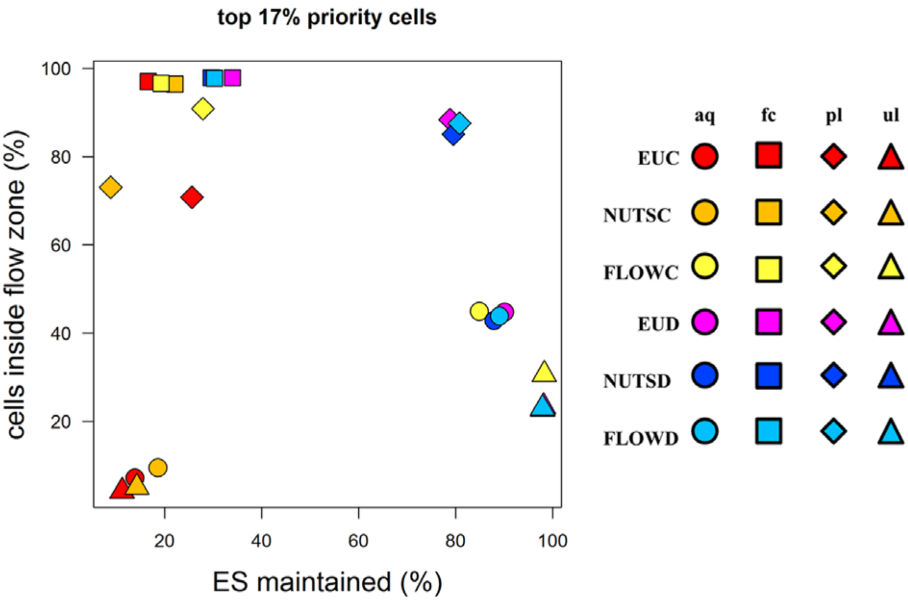

Figure 4. Trade-off between the level of ecosystem services (ESs) maintained and the percentage of priority areas within a flow zone. Results are depicted for the 17% of priority areas that maintain the highest level of ESs (aq, air quality; fc, flood control; pl, pollination; ul, urban leisure). The percentage of cells within flow zones provides an indication of whether priority areas are located in areas where there is an ES demand at present.

Accounting for Flow Zone

For the capacity tests, accounting for flow zone resulted in more evenly spread allocation of top priority areas (Fig. 2 EUC vs. NUTSC vs. FLOWC). The degree of overlap in top-priority areas between EUC and FLOWC tests ranged from 16.64%, for the top 1% priority areas, to 50.77%, for the top 25% priority areas (Supporting Information). The demand tests were much more alike in terms of spatial overlap (Supporting Information) because accounting for demand already reduced the solution space significantly.

The effect of accounting for flow zones varied across ESs. Compared with the EUC test, the NUTSC tests had little effect on the demanded capacity retained for most ESs, and it performed very poorly for pollination. For air-quality regulation and urban leisure, the FLOWC tests (respectively 84.9% and 98.3%) greatly increased the level of ES maintained relative to the NUTSC (18.6% and 14.3%) and EUC (13.9% and 11.2%) tests. Accounting for flow zones barely decreased the level of ES maintained at the EU level for the demand tests (e.g., air-quality EUD 90.1% vs. FLOWD 89.1%) (Fig. 3).

ESs Maintained Per Flow Zone

Both accounting for ES demand and flow zones affected the distribution of priority areas across flow zones (Fig. 4) and the level of ES maintained per flow zone (Fig. 5). Results differed among ESs. For air quality and urban leisure, the EUC and NUTSC tests performed similarly; both had low levels of ES maintained and a low percentage of priority areas within flow zones. The other 4 tests showed a high level of ES maintained and a high percentage of cells within flow zones. A similar pattern was observed for the distribution of ESs across flow zones (Fig. 5). At 17% priority areas, there was no effect of accounting for demand on the distribution of ESs across flow zones because 100% of the ESs were already maintained. In the EUC test, 26.6% of the flow zones had no ES maintained. In the FLOWC and demand tests, all flow zones had at least some ES maintained. At 5% or 10% priority areas there was a redistribution of ES maintained across flow zones (Supporting Information).

For flood regulation and pollination, there was a clear difference between the capacity and demand tests. All tests had a high percentage of priority areas within flow zones, mainly because the flow zones covered almost all of Europe. The FLOWC test performed similar to the other capacity tests, although for pollination more cells were maintained within flow zones. Accounting for ES demand clearly increased the level of ES maintained, but there was no clear difference between the demand tests (Figs. 4 & 5). Of the demand tests FLOWD had a relatively high median and the lowest variation of the demand tests, meaning priority areas were more evenly distributed over flow zones. Moreover, accounting for the flow zone (FLOWD vs. EUD) reduced the amount of flow zones with no ES maintained for flood regulation (8.9%) and pollination (14.3%) (Supporting Information).

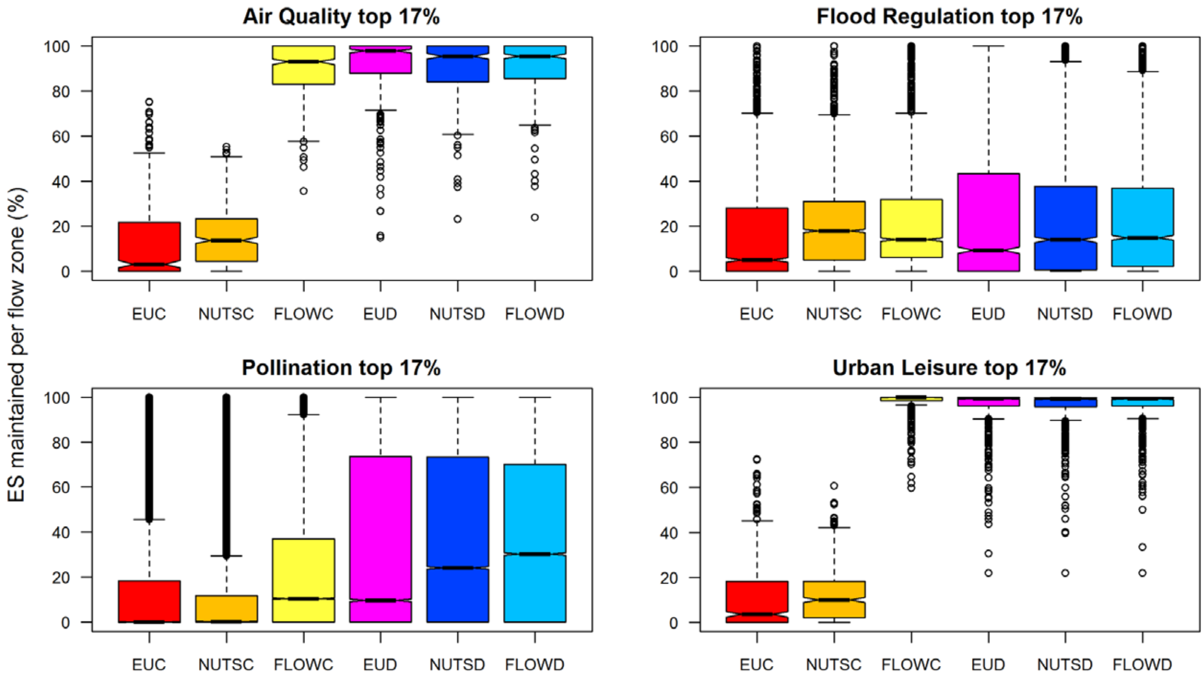

Figure 5. Percentage of ecosystem services (ESs) maintained per flow zone for the 4 ecosystem services for each test (x-axis; tests defined in Methods). A small bar (colored area) and a high median (black lines) indicates a relatively even distribution of the level of ESs maintained per flow zone. Dashed lines indicate the value at 1.5 times the interquartile range (i.e., the difference between the minimum and maximum value of the bar). Values outside this range are often outliers (circles). Circles indicate flow zones that have far higher or lower levels of ES maintained than could be expected based on the spread of the data. The results shown are for the 17% of priority areas that maintain the highest level of ESs. Figures for different percentages of priority areas are in Supporting Information.

The Flow Zone as a Proxy for ES Demand

Overall only FLOWC tests showed that it was possible to use flow zones in combination with ES capacity maps as a proxy for ES demand. Spatially, the NUTSC test caused a larger spread of priority areas compared with the EUC test (Fig. 2), but this attempt to better distribute priority areas among areas of demand also resulted in priority areas in regions with little demanded capacity (Fig. 3). Results of the FLOWC test closely resembled those of the demand tests. The overlap in priority areas between all demand tests and the FLOWC test ranged from 22.3% for the 1% priority areas to 62.3% for the 25% priority areas.

The FLOWC test increased the level of ES maintained for air quality and urban leisure and thus performed similarly to the demand tests (Fig. 3). The FLOWC test resulted in less of an improvement for the other ESs. The NUTS test did not increase the ES maintained per flow zone relative to the EUC test for all ESs.

Discussion

We aimed to quantify the importance of accounting for the demand and flow zone of ESs in identifying priority areas. We found that accounting only for ES capacity data resulted in priority areas high in ecosystem functioning, but these areas would not actually provide ESs to society. In particular, for local ESs, it was important to consider the fraction of the capacity that fulfilled a demand, rather than capacity per se. Our findings are consistent with research on ES conservation in Canada, where priority areas for ES capacity maintained 20–50% of the proportion of ES demanded capacity for local ES (Cimon-Morin et al. 2014).

Because benefits from local and regional ESs need to be distributed across the EU, we assessed the effect of accounting for flow zones. We moved beyond the traditional way of evaluating priority areas for efficiency at the study scale by including metrics on the spatial distribution of ESs and priority areas. Accounting for flow zones changed the location of priority areas. The redistribution of priority areas across flow zones did not affect the level of ES maintained but did result in a reduction of flow zones without any ES maintained. Moreover, accounting for flow zones resulted in the level of ES maintained per flow zone to become more alike. This effect was strongest for small priority networks for air quality and urban leisure and for large priority networks for flood regulation and pollination. In general, accounting for the flow zone resulted in a more even distribution of ES maintained across the EU without a clear decrease in the total level of ES maintained. Nevertheless, the effect of accounting for flow zones was small and the effect differed among ESs. Previous research mostly ignores flow zones in prioritization (Casalegno et al. 2014; Cimon-Morin et al. 2014). Chan et al. (2006) identified flow zones per ES but did not test the effect of accounting for flow zones on ES prioritization. In a previous application of Zonation, administrative units were used to distribute priority areas across regions (Moilanen & Arponen 2011; Pouzols et al. 2014). With our approach it is possible to combine ES-specific flow zones within spatial prioritization.

Although ES demand is more frequently mapped nowadays (Wolff et al. 2015), maps for ES demand and ES flow are not commonly available. We showed that for prioritization ES-specific flow zones (FLOWC) can be used as a proxy for ES demand, particularly for local-flow ESs in the absence of demand data (Fig. 3). Using administrative units as a generic proxy for demand (NUTSC) did not provide equally good results in terms of maintenance of ES demanded capacity (Fig. 3).

Approach

We considered 5 ESs for which both ES capacity and ES demand data were available. Our results were partly driven by our selection of ESs. Ecosystem service demand is especially high close to cities, and our priority network was strongly driven by demand for air quality, urban leisure, and to a lesser extent flood regulation. To fully assess the efficiency of the prioritized areas, the over- and undersupply of ESs per flow zone or for the EU would be interesting to consider. However, such an analysis was not possible because ES demand and ES capacity data were not measured in the same units, except for air-quality regulation. Our approach to calculating demand capacity is straightforward and easy to implement for all ES flows, as long as there is an estimate of demand that is spatially explicit.

Flow zones are not commonly used in prioritization studies. Delineation of flow zones was, except for pollination, based on previous studies and existing spatial planning units. Chan et al. (2006) identified flow zones using similar delineation methods including catchments (flood control) and city surroundings (recreation). Chan et al. (2006) did not identify flow zones for pollination because of uncertainties in foraging distances of pollinators. More detailed delineation of flow zones and accounting for the uncertainty in current delineations could further improve these assessments.

A full ES prioritization needs to incorporate additional variables such as management costs, human-based alternatives for ESs, and threats to ES supply (Luck et al. 2012). We used area as a costs measure, as has been done by others (Casalegno et al. 2014; Pouzols et al. 2014). Nonuniform costs can be assessed through costs for land acquisition and land management (Naidoo et al. 2006; Remme & Schröter 2016) or through costs of foregone production (Schröter et al. 2014). Land costs could be approximated using land prices or, if not available, using population density or gross domestic product as a proxy. Land prices are likely higher around cities and could therefore conflict with priority areas after accounting for ES demand. Our results indicated that, in spite of the potential costs, priority areas for ESs are likely to remain close to cities given the high ES demand in and around cities. Therefore, we consider our result that accounting for demand causes large shifts in priority areas robust.

We did not account for land-use change or other threats to ESs. Land-use change can affect both ES capacity and demand (Stürck et al. 2015). For example, increases in biofuel crops, such as rapeseed, may increase the pollination dependency of current croplands. Land-use change may result in threats to ESs (urban expansion) but could also provide opportunities for restoration of ESs following land abandonment.

There are important differences between Zonation, as we used it, and other spatial prioritization software such as Marxan (Possingham et al. 2000). Zonation generates a priority ranking throughout the study area instead of trying to achieve a target-based solution (Lehtomäki & Moilanen 2013). Zonation is most useful when individual targets cannot be easily determined (Lehtomäki & Moilanen 2013), as is the case for most ESs (Remme & Schröter 2016). Accounting for flow zones is possible in target-based planning software such as Marxan. In a study in California, Chan et al. (2006) accounted for flow zones of ESs by assigning unique conservation targets to different zones in Marxan.

Policy Implications

Our outcomes have important consequences for policies aimed at protecting biodiversity and ESs. Accounting for the flow zone of ESs resulted in smaller and more scattered priority areas. For biodiversity conservation larger clustered protected areas are preferred because of management efficiencies and species habitat requirements (Van Teeffelen et al. 2006). Moreover, coordinated identification of priority areas results in more efficient solutions for biodiversity conservation (Pouzols et al. 2014; Kukkala et al. 2016). Priority areas for biodiversity conservation also need to balance efficient biodiversity protection and the distribution of biodiversity conservation across a region. The most efficient protected-area network could simultaneously create a politically and biologically undesirable outcome if it does not result in maintaining well-functioning natural systems across an area (Moilanen & Arponen 2011).

The need to protect biodiversity at a global scale and ESs at smaller scales therefore does not have to be at odds.

Most importantly, our results clearly show that ignoring ES demand leads to the identification of priority areas in remote regions, where benefits to society are small. Incorporating ESs in conservation planning should therefore always account for ES demand to avoid inefficient solutions.

Acknowledgments

We thank P. Vizcaino from JRC for access to the air-quality data, J. Sturck for access to the food-regulation data, and N. Schulp for access to the pollination and carbon-sequestration data. W.V., A.v.T., and P.V. acknowledge financial support from the European Union Seventh Framework Programme (FP7/2007–2013) under grant agreement 308393 OPERAs. A.M. thanks the Academy of Finland Centre of Excellence program 2012–2017 and the Finnish Ministry of Environment for support and KONE foundation for financial support.

Supporting Information

Additional figures (Appendix S1), methods on urban leisure capacity (Appendix S2), and zonation setup and setting files (Appendix S3) are available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

Literature Cited

Bubeck P, de Moel H, Bouwer LM, Aerts JCJH. 2011. How reliable are projections of future flood damage? Natural Hazards and Earth System Sciences **11**: 3293–3306.

Casalegno S, Bennie JJ, Inger R, Gaston KJ. 2014. Regional scale prioritisation for key ecosystem services, renewable energy production and urban development. PLOS ONE **9** (e3107822) DOI:10.1371/journal.pone.0107822.

Chan KMA, Shaw MR, Cameron DR, Underwood EC, Daily GC. 2006. Conservation planning for ecosystem services. PLOS Biology **4** (e379) DOI:10.1371/journal.pbio.0040379.

Cimon-Morin J, Darveau M, Poulin M. 2013. Fostering synergies between ecosystem services and biodiversity in conservation planning: a review. Biological Conservation **166:**144–154.

Cimon-Morin J, Darveau M, Poulin M. 2014. Towards systematic conservation planning adapted to the local flow of ecosystem services. Global Ecology and Conservation **2:**1–13.

Convention on Biological Diversity (CBD). 2010. Strategic plan for biodiversity 2011-2020 and the Aichi Targets. CBD Secretariate, Montreal.

Derkzen ML, van Teeffelen AJA, Verburg PH. 2015. Quantifying urban ecosystem services based on high-resolution data of urban green space: an assessment for Rotterdam, the Netherlands. Journal of Applied Ecology **52:**1020–1032.

Durán A, Duffy J, Gaston K. 2014. Exclusion of agricultural lands in spatial conservation prioritization strategies: consequences for biodiversity and ecosystem service representation. Proceedings of Royal Society B: Biological Sciences **281:**20141529.

EEA (European Environment Agency). 2008. European river catchment (ERC) classified by ocean. EEA, Copenhagen. Available from http://www.eea.europa.eu/data-and-maps/data/european-river-catchments-1#tab-gis-data (accessed June 2015).

European Commission. 2013. Green infrastructure (GI) — enhancing Europe's natural capital. COM(2013)249 final. Commission of the European Communities, Brussels.

European Commission. 2011. Our life insurance, Our natural capital: an EU biodiversity strategy to 2020. European Commission, Brussels.

Fisher B, Turner RK, Morling P. 2009. Defining and classifying ecosystem services for decision making. Ecological Economics **68:**643–653.

GISCO (Geographic Information System of the Commision). 2011. Urban audit. GISCO, Luxembourg. Available from http://ec.europa.eu/eurostat/web/gisco/geodata/reference-data/administrative-units-statistical-units/urban-audit (accessed September 2015).

Kukkala AS, Arponen A, Maiorano L, Moilanen A, Thuiller W, Toivonen T, Zupan L, Brotons L, Cabeza M. 2016. Matches and mismatches between national and EU-wide priorities: examining the Natura 2000 network in vertebrate species conservation. Biological Conservation **198:**193–201.

Lehtomäki J, Moilanen A. 2013. Methods and workflow for spatial conservation prioritization using Zonation. Environmental Modelling and Software **47:**128–137.

Luck GW, Chan KM, Klien CJ. 2012. Identifying spatial priorities for protecting ecosystem services. F1000 Research DOI: 10.12688/f1000research.1-17.v1.

Maes J, Lavalle C, Vizcaino Martinez P. 2015. LF511- NO2 removal by urban vegetation (LUISA Platform REF2014). European Commission, Joint Research Centre. Available from http://data.europa.eu/89h/jrc-luisa-lf511-no2-removal-by-urban-vegetation-ref-2014 (accessed June 2014).

Maes J, Liquete C, Teller A, Erhard M. 2016. An indicator framework for assessing ecosystem services in support of the EU Biodiversity Strategy to 2020. Ecosystem Services **17:**14–23.

MEA (Millenium Ecosystem Assessment). 2005. Ecosystems and human well-being: synthesis. Island Press, Washington, D.C.

Moilanen A, Arponen A. 2011. Administrative regions in conservation: Balancing local priorities with regional to global preferences in spatial planning. Biological Conservation **144:**1719–1725.

Moilanen A, Franco AMA, Early RI, Fox R, Wintle B, Thomas CD. 2005. Prioritizing multiple-use landscapes for conservation: methods for large multi-species planning problems. Proceedings of the Royal Society B Biological Sciences **272:**1885–1891.

Moilanen A, Pouzols FM, Meller L, Veach V, Arponen A, Leppänen J, Kujala H. 2014. Spatial conservation planning methods and software Zonation. User manual. Version 4. Helsinki.

Moilanen A, Wilson KA, Possingham HP. 2009. Spatial conservation prioritization: quantitative methods and computational tools. Oxford University Press, Oxford, United Kingdom.

Naidoo R, Balmford A, Ferraro PJ, Polasky S, Ricketts TH, Rouget M. 2006. Integrating economic costs into conservation planning. Trends in Ecology & Evolution **21:**681–687.

Orsi F, Church RL, Geneletti D. 2011. Restoring forest landscapes for biodiversity conservation and rural livelihoods: a spatial optimisation model. Environmental Modelling and Software **26:**1622–1638.

Paracchini ML, Zulian G, Kopperoinen L, Maes J, Schägner JP, Termansen M, Zandersen M, Perez-Soba M, Scholefield PA, Bidoglio G. 2014. Mapping cultural ecosystem services: A framework to assess the potential for outdoor recreation across the EU. Ecological Indicators **45:**371–385.

Pistocchi A, Marinov D, Pontes S, Zulian G, Trombetti M. 2011. Multimedia assessment of pollutant pathways in the environment: a global scale model. Joint Research Centre, Luxembourg.

Possingham HP, Ball IR, Andelman SJ. 2000. Mathematical methods for identifying representative reserve networks. Pages 291–305 in Ferson S, Burgman MA, editors. Quantitative methods for conservation biology. Springer Verlag, New York.

Pouzols FM, Toivonen T, Di Minin E, Kukkala AS, Kullberg P, Kuusterä J, Lehtomäki J, Tenkanen H, Verburg PH, Moilanen A. 2014. Global protected area expansion is compromised by projected land-use and parochialism. Nature **516:**383–386.

Remme RP, Schröter M. 2016. Effects of budget constraints on conservation network design for biodiversity and ecosystem services. Ecological Complexity **26:**45–56.

Schröter M, Rusch GM, Barton DN, Blumentrath S, Nordén B. 2014. Ecosystem services and opportunity costs shift spatial priorities for conserving forest biodiversity. PLOS ONE **9** (e112557) DOI:10.1371/journal.pone.0112557.

Schulp CJE, Lautenbach S, Verburg PH. 2014. Quantifying and mapping ecosystem services: Demand and supply of pollination in the European Union. Ecological Indicators **36:**131–141.

Schulp CJE, Nabuurs G-J, Verburg PH. 2008. Future carbon sequestration in Europe—Effects of land use change. Agriculture, Ecosystems & Environment **127:**251–264.

Stürck J, Poortinga A, Verburg PH. 2014. Mapping ecosystem services: the supply and demand of flood regulation services in Europe. Ecological Indicators **38:**198–211.

Stürck J, Schulp CJE, Verburg PH. 2015. Spatio-temporal dynamics of regulating ecosystem services in Europe – the role of past and future land use change. Applied Geography **63:**121–135.

Van Berkel DB, Verburg PH. 2011. Sensitising rural policy: assessing spatial variation in rural development options for Europe. Land Use Policy **28:**447–459.

Van der Zanden EH, Verburg PH, Mücher CA. 2013. Modelling the spatial distribution of linear landscape elements in Europe. Ecological Indicators **27:**125–136.

Van Teeffelen AJA, Cabeza M, Moilanen A. 2006. Connectivity, probabilities and persistence: comparing reserve selection strategies. Biodiversity and Conservation **15:**899–919.

Wolff S, Schulp CJE, Verburg PH. 2015. Mapping ecosystem services demand: a review of current research and future perspectives. Ecological Indicators **55:**159–171.