

CONSERVATION

Balancing conservation priorities for nature and for people in Europe

Louise M. J. O'Connor^{1*}, Laura J. Pollock^{1,2}, Julien Renaud¹, Willem Verhagen^{3,4}, Peter H. Verburg^{3,5}, Sandra Lavorel¹, Luigi Maiorano⁶, Wilfried Thuiller¹

There is an urgent need to protect key areas for biodiversity and nature's contributions to people (NCP). However, different values of nature are rarely considered together in conservation planning. Here, we explore potential priority areas in Europe for biodiversity (all terrestrial vertebrates) and a set of cultural and regulating NCP while considering demand for these NCP. We quantify the spatial overlap between these priorities and their performance in representing different values of nature. We show that different priorities rarely coincide, except in certain irreplaceable ecosystems. Notably, priorities for biodiversity better represent NCP than the reverse. Theoretically, protecting an extra 5% of land has the potential to double conservation gains for biodiversity while also maintaining some essential NCP, leading to co-benefits for both nature and people.

There have been recent policy calls to expand protection to at least 30% of the world's area by 2030 to halt the extinction of species and degradation of nature's contributions to people (NCP) (1, 2), but exactly where and how to focus conservation efforts is unclear (3). Biodiversity underpins functioning ecosystems, which sustain NCP essential to human life (4, 5). These include critical regulating NCP, such as pollination, carbon sequestration, flood prevention, and regulation of air quality. Beyond material benefits, ecosystems also contribute to invaluable parts of human culture: Foraging for wild foods, nature-based tourism, and heritage landscapes are examples of cultural NCP (5). Protected areas have been shown to safeguard not only biodiversity (6) but also regulating and cultural NCP (7). However, although they are conceptually linked, different values of nature [intrinsic, cultural, and regulating (fig. S1)] are likely to be tied to different conservation outcomes (8, 9). So, how can we maximize conservation gains across the spectrum of nature's values?

There is a need to conserve key, irreplaceable ecosystems that are not only particularly diverse but that also sustain rare species and provide locally valuable NCP. So far, few studies have combined biodiversity and NCP in spatial conservation planning at large spatial scales (8–10). Many conservation studies place high

value on exceptionally biodiverse locations, which risks overlooking endemic or threatened species (11) and might not lead to the most efficient selection of sites (e.g., if biodiverse sites all contain similar species). Consideration of irreplaceability and complementarity between priority areas is crucial to maximize conservation gains in limited amounts of land (12, 13).

Spatial conservation planning also needs to account for existing protected areas. In Europe, high levels of habitat fragmentation and a long history of human development have shaped the continent's biodiversity. Natura 2000, the densest network of protected areas on the planet (fig. S2), incorporates a diversity of management practices, from strict nature reserves to multiuse areas. This variety of management types is relevant for the conservation of different values of nature, especially in a context where human-induced environmental changes already dominate landscapes. However, the designation and management of Natura 2000 protected areas only consider certain rare species and ecosystem types, do not explicitly consider NCP (14), and have been repeatedly criticized for not integrating local beneficiaries (15).

Here, in line with the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services framework (5, 16) and based on the principles of complementarity and irreplaceability, we contrast conservation priorities at 1-km² resolution for three important values of nature in Europe (fig. S1): (i) biodiversity, represented here by all 785 vertebrate species occurring in the study area, including 124 threatened species (fig. S3); (ii) regulating NCP, represented here by carbon sequestration, air quality regulation, flood control, and pollination (fig. S4); and (iii) cultural NCP, represented here by heritage agriculture, heritage forests, foraging areas for wild foods, and nature tourism (fig. S5 and table S1) (17). We considered the demand for NCP, so that

NCP priorities are ecosystems where a high capacity of providing NCP coincides with a high demand, consistent with the Convention on Biological Diversity targets (18). We first identified spatial priorities separately for each value (species, cultural, and regulating NCP) for the entire European Union (EU) regardless of protection status, and we quantified the incidental gains and losses for different nature values within these top priorities. Second, we assessed how well these values of nature are currently represented in the Natura 2000 network of protected areas. As a preliminary step to integrate multiple values of nature into conservation planning, we identified priorities outside Natura 2000 that would best complement the existing network.

We found that, in an optimal allocation of EU land for conservation, top priorities (the highest-ranked 10% of area) for different values of nature rarely coincide: Areas where top priorities for two values overlap cover 3.2% of EU land, and areas where top priorities for all three values overlap only cover 0.29% of EU land, mostly in Mediterranean woodlands (Fig. 1, A and B; and fig. S9A). Cultural benefits are gained linearly as more area is protected (Fig. 2C and fig. S10A), because of the broad spatial distribution of the cultural NCP considered here. On the contrary, for the vertebrate species and the regulating NCP considered, a few key areas could yield high conservation gains (Fig. 1C and fig. S10A), but not in the same places. Top 10% priorities for species include on average 39% (SE = 1.2%) of all species distributions [including 59% of threatened species distributions but only 10% of regulating NCP (Fig. 1C and fig. S11)], and they are mostly located in Mediterranean countries, Eastern Europe, and Scandinavia (Fig. 1A and fig. S12). By contrast, top priority areas for regulating NCP (Fig. 1C) include on average 42% (SE = 11%) of key ecosystems for the regulating NCP considered (but only 9.5% of all species distributions) and are mostly located in forests of Romania, seminatural habitats of Spain, peri-urban vegetation in Sweden, and riparian ecosystems in central Europe (Fig. 1A and figs. S9A and S12). This analysis shows that simultaneously conserving vertebrate species and regulating NCP can only be achieved through considering them both. Further, species priorities coincide more often with cultural priorities than with regulating priorities (Fig. 1B and figs. S13 and S18) and incidentally represent a much higher proportion of threatened species distributions than priorities for regulating NCP (Fig. 1C and fig. S11). Even though species priorities do not optimally represent regulating NCP, the losses in relation to the optimal representation are smaller when prioritizing species than when prioritizing regulating NCP (Fig. 1C and fig. S19). Our results suggest that focusing on species

¹Univ. Grenoble Alpes, Univ. Savoie Mont Blanc, CNRS, LECA, Laboratoire d'Écologie Alpine, F-38000 Grenoble, France.

²Department of Biology, McGill University, Montreal, QC H3A 1B1, Canada. ³Environmental Geography Group, Institute for Environmental Studies, Vrije Universiteit Amsterdam, De Boelelaan 1085, 1081HV Amsterdam, Netherlands. ⁴Frederick S. Pardee Center for International Futures, Josef Korbel School of International Studies, University of Denver, Denver, CO 80208, USA. ⁵Swiss Federal Research Institute WSL, Zürcherstrasse 111, CH-8903 Birmensdorf, Switzerland. ⁶Department of Biology and Biotechnologies "Charles Darwin," University of Rome "La Sapienza," Rome, Italy.

*Corresponding author. Email: louise.m.j.oconnor@gmail.com

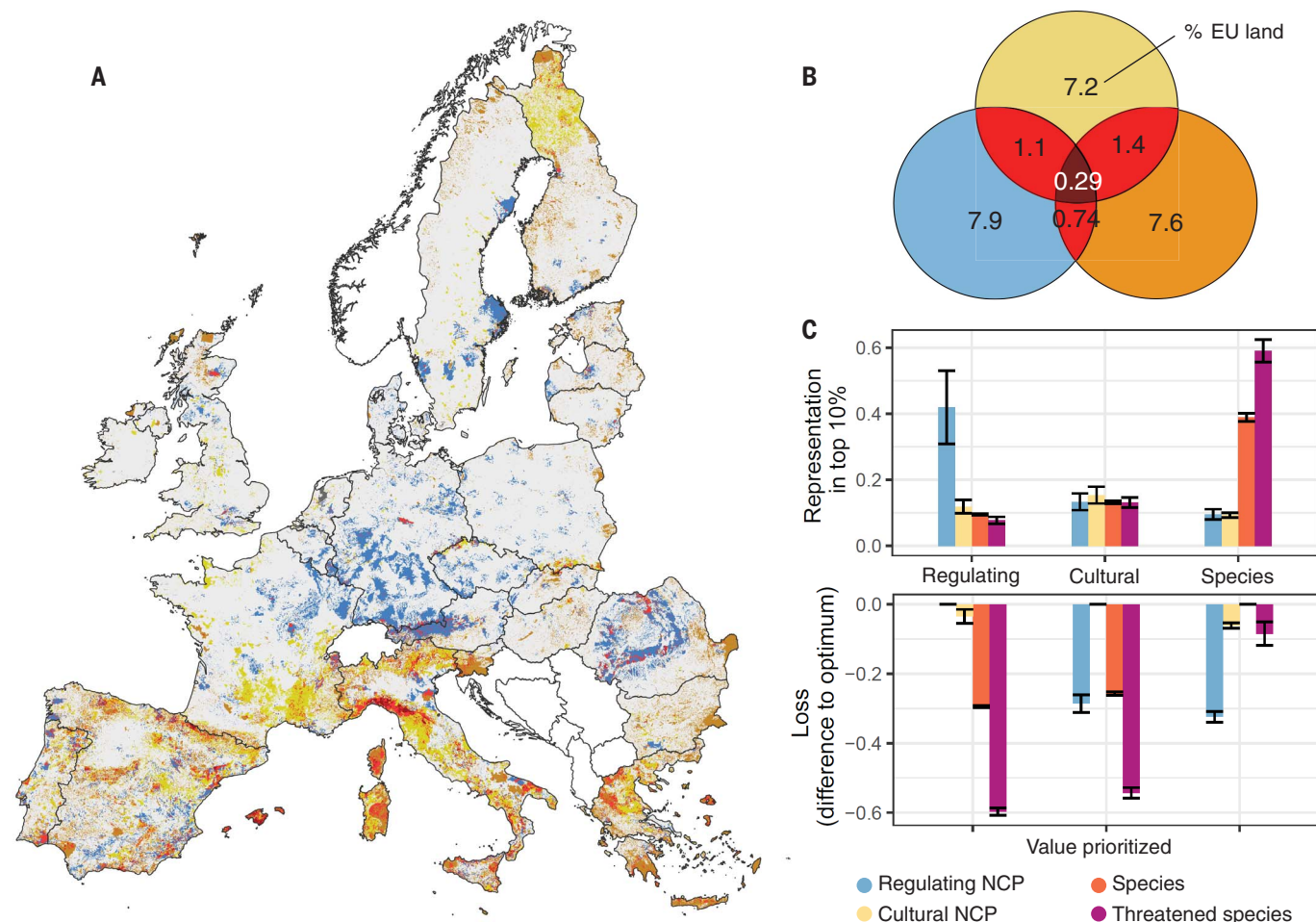


Fig. 1. Spatial coverage and ecological value of top 10% priorities in the optimal scenario. (A) Map locating the top 10% priorities for all three nature's values considered. Top priorities for vertebrate species are shown in orange, cultural NCP are in yellow, and regulating NCP are in blue. Areas of overlap between top priorities for two different values are bright red (3.2% of entire study region); areas of overlap between top priorities for all three values are brown (0.29% of entire study region). (B) Percentages of the study region (EU27)

covered by different priorities and areas of spatial overlap. Color scheme is the same as in (A). (C) Bar plots quantifying the proportion of all distributions represented (y axis) in the top 10% of each prioritization (x axis) on average (error bars represent the SE) and the corresponding loss (i.e., the difference between the incidental representation in the prioritization and the optimal representation of a given value). The colors represent the value: magenta, threatened species; orange, all species; yellow, cultural NCP; blue, regulating NCP.

could be more effective to maximize conservation gains across the spectrum of nature's values than any other value considered here (fig. S19). These results are robust to variations in the top priority threshold, input data, and spatial resolution (figs. S13 to S19).

A gap analysis revealed that half of the Natura 2000 sites are of high conservation value (the highest-ranked 5% of area within the network) for species, regulating, and cultural NCP. A quarter of these top priorities overlap for at least two values (Fig. 2, A and B), mostly in Mediterranean countries (fig. S12). Half of these "protected" cells of high conservation value actually contain less than 100 ha of Natura 2000 (Fig. 2B and figs. S10B and S20). However, despite covering one-fifth of EU land, Natura 2000 does not optimally represent any of nature's values considered here. On average, 70% of key ecosystems for regulating NCP and 64% of all vertebrate

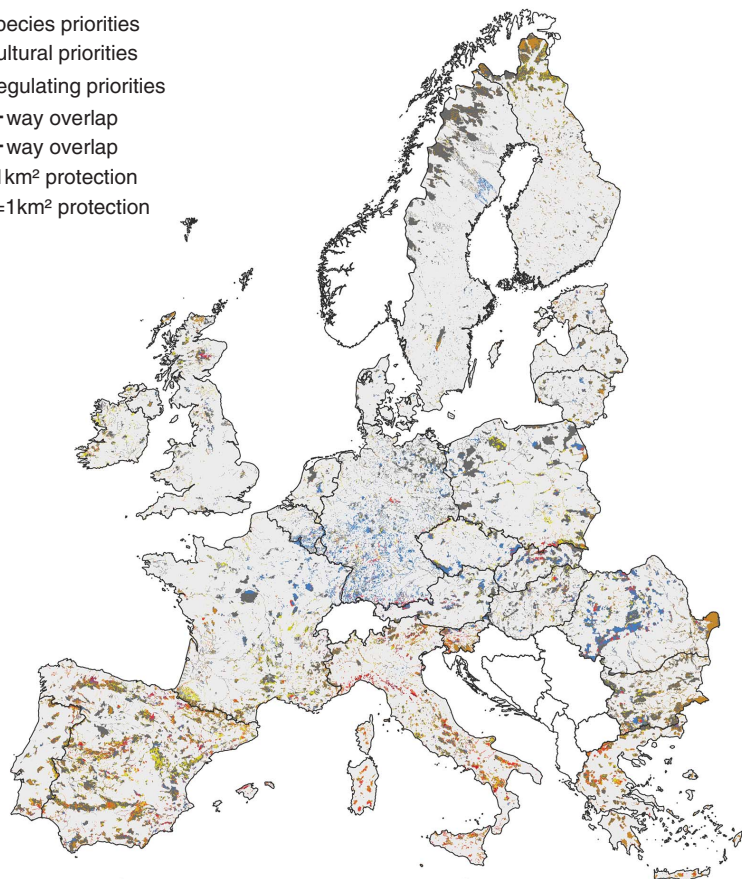
species' ranges (and 57% of threatened species' ranges) are not protected (Fig. 2, D to F). Our results suggest that large conservation gains are within reach: If the Natura 2000 network were to be expanded by 5%, the protection of species and key ecosystems for the considered NCP would become equivalent to the optimal scenario (Fig. 2, D to F). If protected, these key areas have the potential to double the current representation of vertebrate species and of regulating NCP in Natura 2000 and also to protect almost 75% of threatened species ranges on average. Locations that complement the existing Natura 2000 areas simultaneously for species and NCP represent 1.38% of EU land, and they are concentrated in Mediterranean woodlands and extensive agricultural areas (Fig. 2C and fig. S9B). This analysis is a preliminary step to integrate different values of nature into conservation planning, but it demonstrates that the protection of small, but

well-selected, areas can yield large benefits to both species and NCP.

Here, we harnessed fundamental principles of spatial conservation planning while recognizing the multiplicity of relationships that link humans to nature (5) at a continental scale. Despite fundamental differences between key ecosystems for species and NCP, our results indicate that top priorities for species incidentally represent NCP better than the reverse (figs. S11 and S19). This is because there are highly irreplaceable areas for species (particularly for rare or endemic species), and vertebrates occur in a diverse set of ecosystems, including those that provide NCP. By contrast, most NCP are more widespread, and priorities for NCP are unlikely to capture the areas crucial for all vertebrates. Most regulating NCP are primarily provided by forests (fig. S9), whereas protecting the full set of European species requires a complementary set of habitats,

- Species priorities
- Cultural priorities
- Regulating priorities
- 2-way overlap
- 3-way overlap
- <1km² protection
- ≥1km² protection

A



C

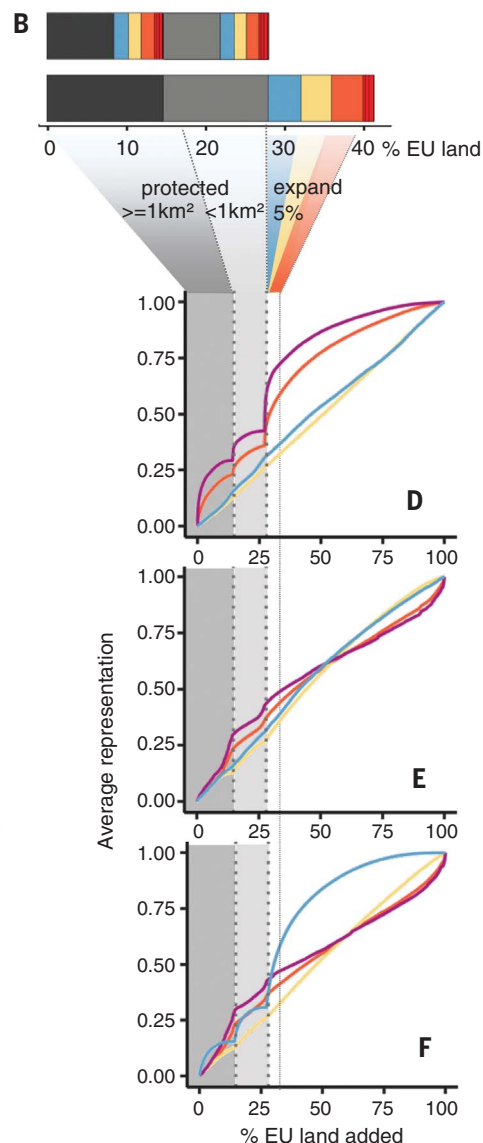
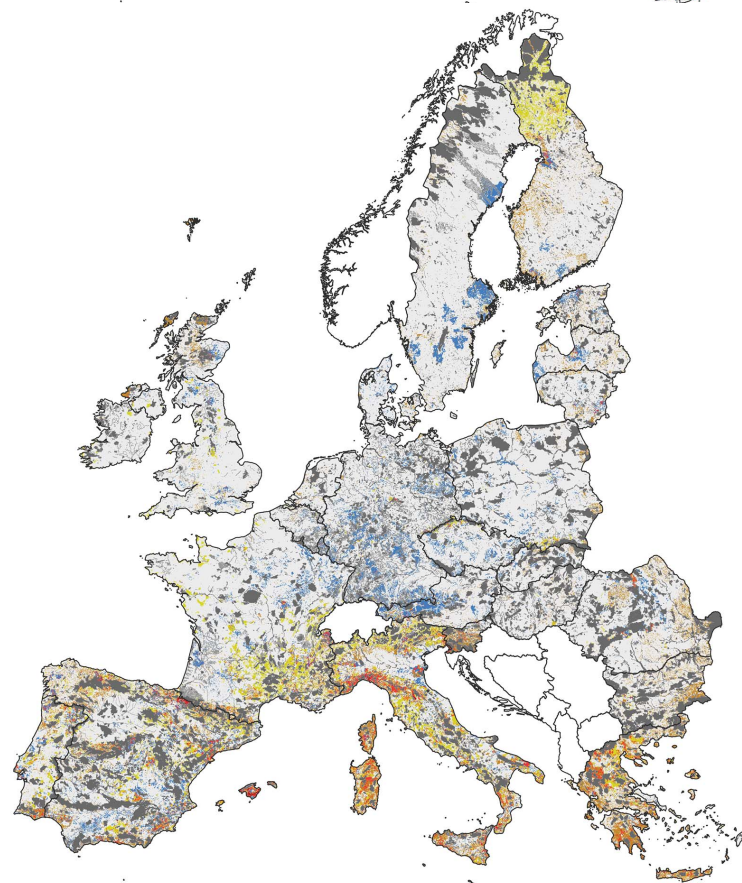


Fig. 2. Key areas for species and NCP within and outside the Natura 2000 protected area network. (A) The top 5% value areas within Natura 2000 sites [both large (dark gray) and small (lighter gray)]. (B) Bar plots quantifying the surface (percentage of EU land) occupied by each type of priority and their spatial overlap for the top 5% of area within Natura 2000 (top) and the top 5% of area outside Natura 2000 (bottom). (C) The top 5% priority areas for the expansion of Natura 2000 for the different nature's values. (D to F) Performance curves accounting for existing Natura 2000 areas, which quantify the representation (average proportion of distributions) gained for each value as land is added in each scenario, prioritizing species (D), cultural NCP (E), and regulating NCP (F). The colors represent the value: magenta, threatened species; orange, all species; yellow, cultural NCP; blue, regulating NCP. The gray shading indicates the land covered by Natura 2000, and the thin vertical line indicates the top 5% threshold for Natura 2000 expansion.

of which forests are only one example, alongside grasslands, bare areas, and aquatic ecosystems (fig. S9). Our findings support recent calls that multiple targets are needed to protect the spectrum of nature's values (19), but we also show that larger conservation gains are possible, in more specific and ecologically diverse areas, when species are prioritized rather than NCP. Furthermore, terrestrial vertebrates have been shown to play a key role in the provision of both cultural and regulating NCP (20, 21), including threatened species (22, 23), which are efficiently represented in top priorities for all species.

The full set of vertebrate species considered here (many of which are understudied) represent a much broader diversity of ecological niches and evolutionary histories than most conservation planning studies, but these species are still only a subset of Earth's biodiversity. A variety of other taxa (invertebrates, plants, fungi, bacteria) and other biodiversity facets, such as functional or phylogenetic diversity (24) (figs. S15 and S18), are even less represented in conservation policies (25). Improving knowledge on the spatial distribution of biodiversity and integrating different ecological datasets are paramount to inform conservation (26). There is a discrepancy between the currently moderate quality of biodiversity data at large spatial scales and the limited areas available for conservation in Europe. Here, we used a resolution of 1 km², which is based on the trade-offs between the uncertainty in species distribution data (17), data on locally valuable NCP (e.g., pollination, air quality regulation), and the needed resolution to be sufficiently relevant for conservation planning. Working at a coarser resolution (e.g., 100 km²) would lead to problems when assessing the Natura 2000 areas (many of which are smaller than 100 ha), especially given the mosaic nature of Europe's landscapes.

Most NCP are currently decreasing except those related to the production of material goods (27). Therefore, protecting key ecosystems that provide cultural and regulating NCP is especially urgent. We identified priorities where high NCP capacity overlaps with high demand, but conserving the capacity of ecosystems to provide NCP independently of current demand can be beneficial. Priority areas could shift in future conditions as a result of shifting human demand for NCP [for instance, with increasing population concentration in Europe's more productive regions (28)]. In addition, pressures such as climate change and habitat loss will further threaten biodiversity and NCP. Improved biodiversity models and innovative con-

servation approaches (29) are needed to protect biodiversity and NCP into the future as species ranges shift and ecosystems are modified (30).

The expansion of agriculture and peri-urbanization restricts wilderness to ever smaller areas, jeopardizing both biodiversity and NCP. In this context, protected areas should exist along a continuum of human presence, from untouched wilderness to sustainable use of nature. In Europe, Natura 2000 allows precisely this flexibility in management, and our results indicate where to ideally expand protection, in ecosystems that potentially sustain a majority of European vertebrate species and some essential NCP. Our results also highlight the potential ecological value of certain small Natura 2000 sites and the borders of larger Natura 2000 sites. Ensuring that these sites are sufficiently large and adequately connected across space will be crucial to sustain ecological processes and maintain viable populations for the long term (31). But to make realistic recommendations for the expansion of protected areas, further issues will need to be addressed. First, different stakeholders need to take part in the process, and economic and opportunity costs for varying sectors should be considered alongside potential ecological value (32). Our prioritization does not include spatial costs (e.g., market value, opportunity costs) (12), which would be necessary to designate protected areas but are likely to reduce the ecological value of the conservation solution (33). Second, the designation of protected areas takes place at national or local levels, despite widespread recognition that spatial prioritization across broader spatial scales (e.g., continents, ecoregions) is more efficient to conserve the total biodiversity across a region (13, 34). In our study, conservation priorities defined at the level of the EU optimize the representation of both species and NCP and would ultimately be more efficient at preventing widespread losses at the continental scale. Finally, our results highlight the complementary roles that different countries need to play to conserve ecosystems for nature and for people (fig. S12) (35). Governing conservation in a concerted manner on much broader taxonomical and geographical scales is crucial to meet global conservation needs but will require mechanisms to efficiently share the responsibilities of conservation management (36).

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SUPPLEMENTARY MATERIALS

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Materials and Methods
Appendices S1 to S4
Figs. S1 to S21
Tables S1 to S4
References (38–59)

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Priorities to protect nature in Europe

There is consensus among conservation scientists that protected areas should be expanded to safeguard biodiversity and ecosystem services, but it is often difficult to prioritize areas for protection. Considering factors that motivate conservation across Europe, an analysis by O'Connor *et al.* includes the value of species, represented by distribution of >800 vertebrate species; the cultural value of landscapes, represented by activities such as nature tourism; and the value of ecosystem services such as carbon sequestration and flood protection. Although these three main features often do not coincide in the landscape, the authors found that a focus on biodiversity in spatial conservation planning is the most effective means of capturing a range of nature's values.

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