Spatial conservation planning for biodiversity and ecosystem services - from concepts and methods to policy agendas in the European Union

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ACADEMIC DISSERTATION

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"We depend on nature for the very air we breathe, for every mouthful of food we consume, for every drop of clean water that we drink."

Sir David Attenborough

ABSTRACT

Conservation of biodiversity and ecosystem services (ES) is one of the greatest challenges of our times. The ultimate role of area-based conservation science and *Systematic Conservation Planning* is to inform on-the-ground spatial planning and decision-making. Computational methods and geographical data resources play an important role in *spatial conservation prioritization*, which is a frequently used analysis for identifying important areas for biodiversity, assessing present protected area networks, or designing future allocations for network expansions. Spatial data based on remote sensing, species distribution modelling, and citizen science have become available, allowing complex spatial analysis with large high-resolution data sets.

Spatial conservation prioritization has introduced several concepts for identifying “the best possible” protected area network. Similarly, protected areas have been an integral part of international conventions, such as the United Nations Convention on Biological Diversity, which has set a quantitative objective for increasing the global protected area coverage to 17 per cent worldwide. Area-based conservation goals are often included in regional biodiversity conservation agendas, such as in the European Union’s (EU) biodiversity strategy to 2020. While policies have increasingly adopted the ES approach for conservation, it is poorly understood how identification of “ES priority areas” should be integrated into spatial conservation planning.

In this thesis, my objective is to dissect the concepts and principles guiding spatial conservation prioritization for biodiversity and ES. I introduce novel methodological solutions in the Zonation software for integrating ES into spatial prioritization. My results show that clarifying the underlying concepts can aid spatial conservation planning. This is crucial especially regarding ES and their successful operationalization in spatial prioritization. Prioritization should always consider demand and connectivity requirements of individual ES. Otherwise, assessments effectively identifying ES priority areas do not necessarily provide timely policy-relevant information.

This work also provides insights on how spatial conservation prioritization, with Zonation applied on modeled high-resolution vertebrate species distribution data, can be used to successfully inform continent-wide conservation policies. The EU-wide Natura 2000 network of protected areas covers moderately well the distributions of a representative group of vertebrate species. Nevertheless, there is a potential efficiency to be gained from additional coordinated conservation planning and future protected area site revisions or additions. While prioritization techniques with explicit spatial data are effective in identifying spatial priorities at the continental scale, conservation efficiency should be considered as part of a wider socio-ecological system. Ultimately, while ES bring spatial conservation planning closer to general land use planning, this work highlights the importance of considering complementary conservation mechanisms and finding more integrative approaches for sustainable land use planning.

Keywords: area-based conservation, biodiversity conservation, ecosystem services, European Union, GIS, Natura 2000 network, optimization, protected areas, systematic conservation planning, spatial prioritization, vertebrate species, Zonation software

TIIVISTELMÄ

Luonnon monimuotoisuuden ja ekosysteemipalveluiden suojelu on yksi aikamme suurimpia haasteita. *Systemaattinen suojelusuunnittelu* kehittyi omaksi tieteenalaksi ennen vuosituhannen vaihdetta ja esitteli erillisen paikkatietoa ja laskennallisia menetelmiä hyödyntävän analyysin, *spatiaalisen suojelupriorisoinnin*. Sen tavoitteena oli alun perin tunnistaa kustannustehokkaasti luontoarvoiltaan monipuolisia ja luonnonsuojeluun sopivia alueita. Luonnonsuojelualueet ovat herättäneet paljon keskustelua myös politiikassa. Esimerkiksi Yhdistyneiden kansakuntien luonnon monimuotoisuutta koskevassa yleissopimuksessa on tavoitteena suojella 17 prosenttia maapallon pinta-alasta. Muita pinta-alaan perustuvia suojelutavoitteita on sisällytetty myös alueellisiin luonnonsuojeluohjelmiin, kuten esimerkiksi Euroopan Unionin (EU) biodiversiteettistrategiaan. Viime aikoina luonnonsuojelupolitiikka on myös alkanut huomioida ekosysteemipalveluja. Sen sijaan ei ole vielä selvää, miten ekosysteemipalveluille voidaan tunnistaa niiden suojelukäyttöön sopivia alueita.

Väitöskirjatutkimukseni pyrkii keskustelemaan, mitkä spatiaalisen suojelupriorisoinnin käsitteet ja menetelmät nousevat keskeisiksi kun tunnistetaan luontoarvoiltaan ja ekosysteemipalveluiltaan arvokkaita alueita. Väitöskirjani arvioi EU:n biodiversiteettistrategian tärkeintä spatiaalista suojelutyökalua, Natura 2000-luonnonsuojelualueverkostoa, käyttämällä menetelmänä spatiaalista priorisointia ja erityisesti Zonation suojelu- ja maankäytön suunnitteluohjelmaa.

Tulokseni osoittavat, että suojelusuunnittelun käsitteiden syvällinen ymmärtäminen ja selventäminen voi edistää sekä priorisointimenetelmien kehittymistä että käytännön suunnittelua. Käsitteiden selkeys on erityisen tärkeää tulosten välittämisessä eri sidosryhmille, mutta erityisesti ekosysteemipalveluiden integroimisessa osaksi suojelusuunnittelua. Ekosysteemipalvelut voidaan sisällyttää yksittäisinä piirrekerroksina suojelupriorisointeihin laji- ja habitaattitietojen rinnalle. Niiden erilaiset spatiaaliset kytkeytyvyysvaatimukset ja todellinen kysyntä olisi kuitenkin huomioitava, jotta priorisoinnit tuottaisivat politiikan ja suunnittelun kannalta mahdollisimman käyttökelpoisia tuloksia.

Väitöskirjani tapaustutkimukset osoittavat, että spatiaalinen suojelupriorisointi menetelmänä, yhdessä eri lähteistä peräisin olevien korkealaatuisten paikkatietoaineistojen kanssa, onnistuu tarjoamaan käyttökelpoista tietoa EU-laajuiseen luonnonsuojelusuunnitteluun ja -politiikkaan. Nykyinen EU-laajuinen Natura 2000-verkosto onnistuu suhteellisen hyvin suojelemaan edustavan määrän selkärankaisia lajeja. Suojelupriorisoinnin avulla voidaan tehokkaasti tunnistaa potentiaalisia alueita luonnonsuojelualueverkoston laajentamiseen. Myös yhteistoiminnallisella rajoja ylittävällä suojelusuunnittelulla pystytään lisäämään suojelun tehokkuutta. Toisaalta luonnonsuojelualueet ja niiden kustannustehokkuus tulisi ymmärtää osana laajempaa sosio-ekologista järjestelmää. Väitöskirjatyöni antaa esimerkkejä siitä, kuinka ekosysteemipalvelut tuovat spatiaalisen suojelusuunnittelun lähemmäs yleistä maankäytön suunnittelua. Suojelusuunnittelu tieteenalana hyötyisi todennäköisesti integroivista, ekologisen ja sosiaalisen kestävyyden huomioivista näkökulmista.

Asiasanat: ekosysteemipalvelut, Euroopan Unioni, GIS, kytkeytyvyys, luonnon monimuotoisuus, luonnonsuojelualueet, luonnonsuojelusuunnittelu, Natura 2000-verkosto,

paikkatieto, selkärankaiset, spatiaalinen optimointi, systemaattinen suojelusuunnittelu, Zonation

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Jerome Bruner, noted Professor and psychologist has offered the advice that one's chances of winning a Nobel Prize increase dramatically by associating with former Nobel winners. Thus, he used to say *"This is obviously not just because the association gives you some "pull" or makes you more visible. It has to do also with your having entered a community in whose extended intelligence you share. It is that subtle "sharing" that constitutes distributed intelligence. By entering such a community, you have entered not only upon a set of conventions of praxis but upon a way of exercising intelligence."* This is something that comes to my mind always when I think about the past six years at the Metapopulation Research Centre (MRC) and my PhD thesis as a learning process. The MRC has been an exceptional community to work, involving a special academic culture and incredible colleagues. They are all people without whom this thesis would not have been possible.

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In Helsinki, February 27, 2017
Aija Kukkala

Contents

List of original publications

This thesis is based on the following publications. The publications are referred to in the text by their roman numerals.

I **Kukkala, A.S.***, Moilanen, A.*, 2013. Core concepts of spatial prioritisation in systematic conservation planning. *Biological Reviews of the Cambridge Philosophical Society* 88(2):443-64.

* The authors have contributed equally.

II **Kukkala, A.S.**, Moilanen, A., 2017. Ecosystem services and connectivity in spatial conservation prioritization. *Landscape Ecology* 32, 5-14.

III **Kukkala, A.S.**, 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.

IV **Kukkala, A.S.**, Santangeli, A., Butchart, S.H.M., Maiorano, L., Ramirez, I., Burfi ld, I.J., Moilanen, A., 2016. Coverage of vertebrate species distributions by Important Bird and Biodiversity Areas and Special Protection Areas in the European Union. *Biological Conservation* 202, 1-9.

V Verhagen, W., **Kukkala, A.S.**, Moilanen, A., van Teeffelen, A., Verburg, P., 2017. Use of demand and spatial flow in prioritizing areas for ecosystem services. *Conservation Biology*, doi: 10.1111/cobi.12872.

	I	II	III	IV	V
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LM: Luigi Maiorano
LZ: Laure Zupan
MC: Mar Cabeza
PC: Peter Verburg
SB: Stuart Butchart
TT: Tuuli Toivonen
WT Wilfried Thuiller
Wv: Willem Verhagen

Abbreviations

ABF	Additive Benefit Function
CAZ	Core Area Zonation
CBD	The United Nations Convention on Biological Diversity
GIS	Geographic information systems
EU	The European Union
ES	Ecosystem services
IBA	Important Bird and Biodiversity Area
N2k	The Natura 2000 network
NGO	Non-governmental organization
PA	Protected area
SCI	Site of Community Interest / Site of Community Importance
SCP	Spatial conservation prioritization
SPA	Special Protection Area

List of figures, boxes and tables

1. INTRODUCTION

The current global trend is that biodiversity is declining at an alarming rate (Butchart et al. 2010, Pereira et al. 2010). It is evaluated that humanity has already transgressed its planetary boundary regarding the rate of biodiversity loss (Rockstrom et al. 2009). The main driver of this process has been massive land use change taking place in all parts of the world (Fischer and Lindenmayer, 2007; Rands et al. 2010) which is expected to escalate further as demand for natural resources continues to increase. Consequent habitat loss, fragmentation, and deterioration have led to the sad fact that many species have become threatened or even extinct (Pimm et al. 2014; Ceballos et al. 2015). While biodiversity loss caused by habitat fragmentation can be immediate or delayed (Krauss et al. 2010; Reich et al. 2012), it will inevitably contribute to change in underlying ecosystem functions and processes (Hooper et al. 2012). Under these circumstances, the status of ecosystems and their services have also been observed to decline (Cardinale et al. 2012). The Millennium Ecosystem Assessment has evaluated that at least 60% of the present global ecosystem services (ES) are being degraded or used unsustainably (MA, 2005). In turn, land use change and urbanization have also been the main drivers for declining ecosystem services (Eigenbrod et al. 2011).

The traditional human response to biodiversity loss has been the establishment of protected areas (PAs) (Rodrigues et al. 2004a; 2004b; Butchart et al. 2012; Watson et al. 2014). While mitigating habitat loss can be understood as a common high-level conservation goal, there are at least two different frameworks, science and policies, that recognize the oldest area-based tool, PAs, as a means of safeguarding biodiversity and ES. However, global biodiversity and ES are not evenly distributed (Brooks et al. 2006; Rodrigues and Brooks, 2007; Naidoo et al. 2008; Butchart et al. 2015). Furthermore, as a result of previous often unintended planning, PAs are highly biased towards economically (and ecologically) unproductive regions (Pressey et al. 1993; Joppa and Pfaff, 2009). Further complicating the issue, there are competing land use interests, meaning that PA establishment may require notable investments as financial costs for the acquisition of land may be high (Ando et al. 1998; Carwardine et al. 2008). Considerable investments may also be required for the future management of these sites (Geldmann et al. 2015). Despite connectivity being identified as important for maintaining species diversity, genetic flo , and ecosystem functions (Hodgson et al. 2011), there is still limited information available on how successfully the present PAs form well-functioning interconnected networks (Juffe-Bignoli et al. 2014). On these grounds, ensuring high quality decisions with respect to PA distribution and coverage represents a major challenge ecologically, politically, and socio-economically.

A scientific framework for systematic conservation planning emerged in the early 1990s to meet the demands for finding more transparent and systematic ways for conservation planning. To date, it is widely recognized as the most influential paradigm to provide decision support for conservation planning (Margules and Pressey, 2000; Pressey and Bottrill, 2009; Sarkar and Illoldi-Rangel, 2010). Systematic conservation planning has introduced several principles and concepts for identifying “the best possible” PA network, complementarity being perhaps the most fundamental one (Justus and Sarkar, 2002). Additional key concepts such as representativeness, irreplaceability, and vulnerability are also frequently used in the field (Ferrier et al. 2000; Margules and Pressey, 2000). Regardless of their relative commonness in the literature of conservation science, there has been vagueness about what exactly these concepts mean and what concepts are important in the field. Within the broader context of systematic conservation planning, there is a distinctive analysis framework frequently called spatial conservation prioritization (SCP; Lehtomäki and Moilanen, 2013). It is a data-driven spatially explicit analysis commonly used for identifying important areas for biodiversity, assessing present PAs, or designing future allocations for PA network expansions (Pouzols et al. 2014). Spatial prioritization can also be used for identifying relevant areas for restoring degraded habitats, for finding areas suitable for impact avoidance, or for biodiversity offsetting (Kareksela et al. 2013; Moilanen, 2013; Nin et al. 2016).

As SCP is a spatially explicit process, identification of optimal conservation areas often turns out to be challenging in computational terms (Sarkar et al. 2006). Spatial prioritization extensively utilizes software tools, such as Marxan (Ball and Possingham, 2000), ConsNet (Ciarleglio et al. 2009) and C-Plan (Pressey et al., 2009). Zonation is a publically available decision support software for spatial conservation and land use planning solving various problems around spatial resource allocation (Moilanen et al. 2005; 2014). In addition to computational software, high-quality geographical data resources are required for successful spatial prioritization. Commonly used data include geo-referenced information on the distribution of biodiversity, for instance distribution maps about species and habitats. Respectively, optional data on costs and land use have been often used (Kullberg and Moilanen, 2014). That said, the role of geographic information science and geographic information systems (GIS) is essential in SCP. Spatial data resources based on field surveys, remote sensing (Nagendra et al. 2013; Rhodes et al. 2015), species distribution modelling (Thuiller et al. 2004), citizen science (Dickinson et al. 2010), and even social media (Di Minin et al. 2015) have become increasingly available, allowing complex spatial analysis with large data sets.

High-level policy decisions around biodiversity conservation do not always involve direct spatial choices (Ferrier and Wintle 2009). Instead, the extent of a PA network is widely used as an indicator of progress towards agreed biodiversity goals. Hence, the objective of increasing the coverage of PAs has been integrated into many conservation agendas at different scales (Chape et al. 2005; EC, 2011a,b; Juffe-Bignoli et al. 2014; UNEP-WCMC and IUCN, 2016). While any conservation objectives, area-based or non-area-based, may be addressed directly via legislation or special biodiversity policy, they may also be more implicitly incorporated into other sectoral policy agendas (e.g. into fisheries or agricultural policies). Conservation objectives can likewise be incorporated into broader sustainability goals or international conventions. When it comes to area-based conservation goals, they are sometimes represented as explicit quantitative area targets, i.e. as a specific percentage of land in a country to be protected (Svancara et al. 2005). The United Nations Convention on Biological Diversity's Aichi target 11 can be interpreted as an area protection target with the aim of increasing the extent of the present terrestrial PAs to 17% globally by 2020 (CBD, 2016). Conservation goals may be also treated in policy agendas in a more feature-specific way, for example by giving priority for certain species. For example, the European Union's biodiversity conservation policy is based on two main pieces of legislation: the Birds and the Habitats Directives (EC, 2011a), which both emphasize conservation within the EU's own ecological network of PAs, in the Natura 2000 network (N2k), which presently represents the most extensive PA system worldwide (EEA, 2012). While the N2k does not set quantitative targets for the area under conservation, the Directives list specific target species and habitats to be protected and the EU Member States are then obliged to conserve and manage these species and habitats in specific sites (Born et al. 2015).

During the last decade both policies and research have shifted focus towards more socio-political approaches in nature conservation. PAs are more frequently expected to create also social and economic benefits (Larsen et al. 2012; Brockington and Wilkie, 2015; Oldekop et al. 2015), reflectin the ongoing progress of PAs becoming more multifunctional and allowing more local resource use (Naughton-Treves et al. 2005). Hence, SCP has increasingly directed attention from solely ecological case studies to socio-political aspects. These approaches employ new methodologies including stakeholder collaborations and social learning, commonly used in policy-making and in other land use planning practices (Knight et al. 2006, 2011). Despite some conceptual similarities, systematic conservation planning as a planning paradigm has been so far relatively isolated from general land use planning (Pierce et al. 2005; Gordon et al. 2009; Reyers et al. 2010).

New socio-political approaches in conservation include also ES. While conservation policies are increasingly employing ES through their protection in priority areas (Maes et al. 2016) ES are findin their way also into SCP (Luck et al. 2012; Schröter et al. 2014a). Yet, ES have been recognized in many policies, including the Convention on Biological Diversity (CBD, 2016) and also for the firs time in the European Union's Biodiversity Strategy to 2020, which refers to ES as "our life insurance, our natural capital" (EC, 2011a). The Intergovernmental science-policy Platform on Biodiversity and Ecosystem Services (IPBES, 2016) also acknowledges ES as important alongside biodiversity. Human well-being is often linked to ES via the ecosystem services cascade model, generating new concepts around ecosystem and human health and green infrastructures (Haines-Young and Potschin 2009; Lafortezza et al. 2013; Liquete et al. 2015). While ES have been identified as important in recent policies, it remains conceptually and operationally unclear how ES should be merged into the SCP process and spatial planning in general (de Groot et al. 2010; Reyers et al. 2010).

Development of theoretical concepts and methods in conservation science may sometimes seem distant from policy-making (Knight et al. 2008; Sutherland et al. 2011). Nonetheless, science and policy are interrelated as ideas and innovations first generated by research later become accepted by and integrated into public policies. Nevertheless, there are major differences in how much policies are evidence-based (Svancara et al. 2005; Game et al. 2015). For instance, the designation of the sites of the European N2k network is an interesting example about a conservation planning process involving both science and policy. In particular, site selection is required to be an interactive process between the Commission and the EU Member States and to be based on agreed scientific criteria. Broadly speaking, the surface area of PAs has increased worldwide covering currently 15% of Earth's terrestrial and inland water surface (UNEP-WCMC and IUCN, 2016). Nevertheless, several countries have reduced their national PA systems (Mascia and Pailler, 2011; Symes et al. 2016). While conservation science and policies may assume PAs to be permanent landscape features, PAs are in reality prone to long-term changes in dynamic and complex socio-ecological systems. Recently, the effectiveness and coherence of the N2k has also been questioned by both science and policy (Born et al. 2015). In conclusion, there is a demand for robust scientific evidence for addressing matters of the present and future PAs (Chape et al. 2005; Butchart et al. 2010; 2012; Kullberg and Moilanen, 2014).

1.1 AIMS OF THE THESIS

Spatial conservation prioritization, protected areas, ecosystem services science, and policy-making may seem like separate themes at first glance. In this thesis, I address these themes outlined in the above introduction and aim at bringing scientifi and policy aspects closer together in terms of spatial conservation planning for biodiversity and ecosystem services. More specificall , I have two types of objectives in this thesis from which conceptual and methodological objectives (a and b) are emphasized in the first two chapters. The third objective (c), focusing on the European Union as a case study area, is emphasized in different ways in the last three chapters. My objectives in this thesis are:

a) To dissect the underlying concepts and principles guiding spatial conservation prioritization.
b) To understand how to integrate ecosystem services into spatial conservation prioritization.
c) To investigate and discuss whether spatial conservation prioritization can be used to inform biodiversity conservation policies and planning in the European Union.

In this thesis, I present five research articles that address the objectives above.

Chapter I aims to understand and define the key concepts and principles of spatial conservation prioritization. The historical backgrounds and meanings of twelve selected concepts are reviewed, identifying first definitions and usages, alternative (and possibly conflicting) later definitions and key applications.

Chapter II focuses on the treatment of connectivity for ES in spatial conservation prioritization, which is a previously largely untreated component of spatial conservation prioritization. This work aims to understand the potential of integrating ES into spatial conservation prioritization. Technical solutions available in the Zonation software applicable for ES are introduced and different types of ES and their connectivity requirements are examined at the conceptual level.

Chapter III investigates whether the EU's biodiversity conservation goals in terms of the main area-based conservation instrument, the Natura 2000 network, have been efficiently achieved. To do this, I apply spatial conservation prioritization and high-resolution modeled vertebrate species distribution data. Coverage of species and spatial patterns of priority areas are compared between the present Natura 2000 network and different alternative planning scenarios at the EU, Member States, and biogeographical levels.

Chapter IV aims to investigate the coverage that the Important Bird and Biodiversity Areas (IBAs) defined by BirdLife International and Special Protection Areas (SPAs) as part of the Natura 2000 network provide to birds and other vertebrates across the EU. First, the aim is to quantify the spatial overlap between SPAs and IBAs, and to infer how well IBAs have served to inform the designation of SPAs. Second, I investigate the representativeness of SPAs and IBAs in covering the distributions of birds as compared with other vertebrates within the EU. Finally, the aim is to identify unprotected areas that could be incorporated into an expanded SPA network to efficientl increase coverage (protection levels) of vertebrate species.

Chapter V deals with ways of accounting for ES demand and flow zones in order to identify

ES priority areas across the EU. This study utilizes mapped capacity and demand data of a global flow (carbon sequestration), a regional flow (flood regulation), and three local flow ES (air quality, pollination, and urban leisure).

2. CONCEPTUAL FRAMEWORK

Theoretically, this thesis finds its position in the interplay of conservation biology, planning geography, and geographical information science. Identifi ation of priority areas for biodiversity has been the main objective in spatial conservation prioritization, which contributes as a key framework in this thesis. In addition, the operational and methodological background essential in this thesis is geographical information science. This work also incorporates theoretical background from the broad field of ecosystem services science and has close relations to biodiversity policies in the EU. Hence, I have divided the overall conceptual framework into 1) scientific and methodological framework, and 2) policy framework. In Figure 1, I place each Chapter of this thesis in the continuum of these two frameworks.

2.1 SCIENTIFIC AND METHODOLOGICAL FRAMEWORK

2.1.1 SPATIAL CONSERVATION PRIORITIZATION AS A TOOL SAFEGUARDING BIODIVERSITY AND ECOSYSTEM SERVICES

2.1.1.1 Area-based conservation science and multiple ways of setting priorities

The ultimate role of conservation science has been to inform on-the-ground planning and decision-making (Ferrier and Wintle 2009; Game et al. 2015). Given that the high-level objective of planning is to secure biodiversity, conservation priorities have frequently been set based on ecological goals.

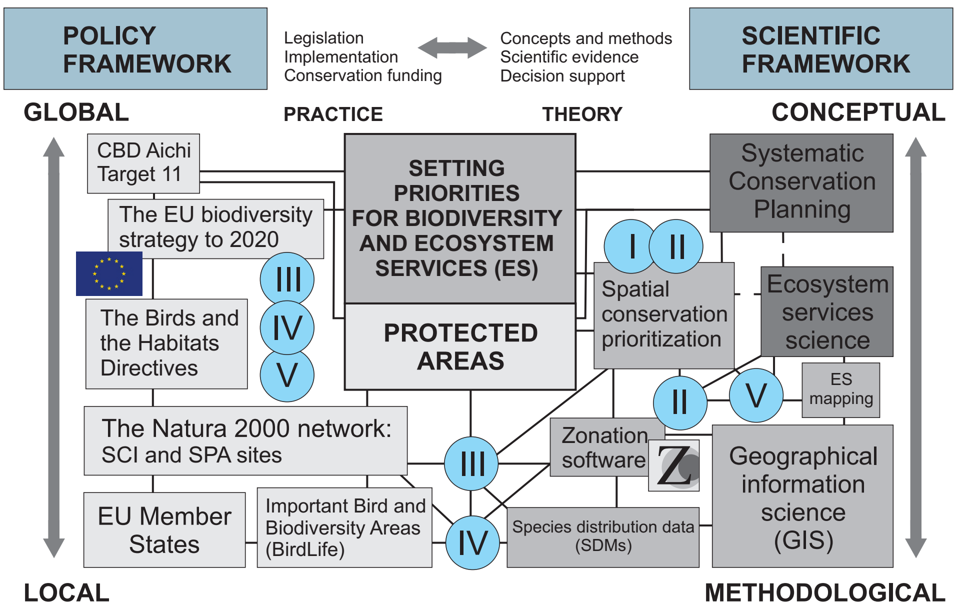


Figure 1. Positioning the thesis within different research and policy frameworks.

As biodiversity is not evenly distributed globally, the essential question in early spatial conservation planning in 1970-90s was formulated at simplest as *where* and *what* to conserve (Vane-Wright et al. 1991; Wilson et al. 2007). As a result, an increasing amount of research emerged trying to fin representative sets of nature reserves (Margules and Usher 1981). Ecologists have long investigated the main drivers of biodiversity loss and paid attention to how diverse spatial characteristics of landscapes (e.g. habitat fragment size, shape, degree of isolation, habitat quality or heterogeneity) influence species persistence, community composition, and ecosystem processes (Connor and McCoy, 1979; Collinge, 1996; Groves and Game, 2016). There are two theoretical developments in spatial ecology that extensively informed area-based conservation science: island biogeography theory (MacArthur and Wilson, 1963) and metapopulation dynamics (Hanski, 1998).

Broadly speaking, there are multiple ways of setting spatial priorities for conservation (Moilanen et al. 2009). Identification of locations of high species richness, "biodiversity hotspots" (Myers et al. 2000), is commonly used for conservation purposes (Margules and Sarkar, 2007). Irreplaceability measures, such as the number of endemic, rare, or threatened and endangered species (e.g. according to the IUCN Red Lists of threatened species; Mace et al. 2008) are frequently used indicators of biodiversity importance as well. Connectivity is repeatedly recognized as an important concept, not only because of the logistics of establishing and managing conservation areas, but also as locations close to each other in the landscape facilitate species' dispersal and implicitly reduce the probability for species' extinction (Hanski 1998; Wilson et al. 2009; Hodgson et al. 2011). Gap analysis, aiming to identify species or other features adequately covered or missed by a given PA network, is one of the most influential methods in conservation planning (Rodrigues et al. 2004a). Population viability analysis is yet another common method in the field (McCarthy, 2009).

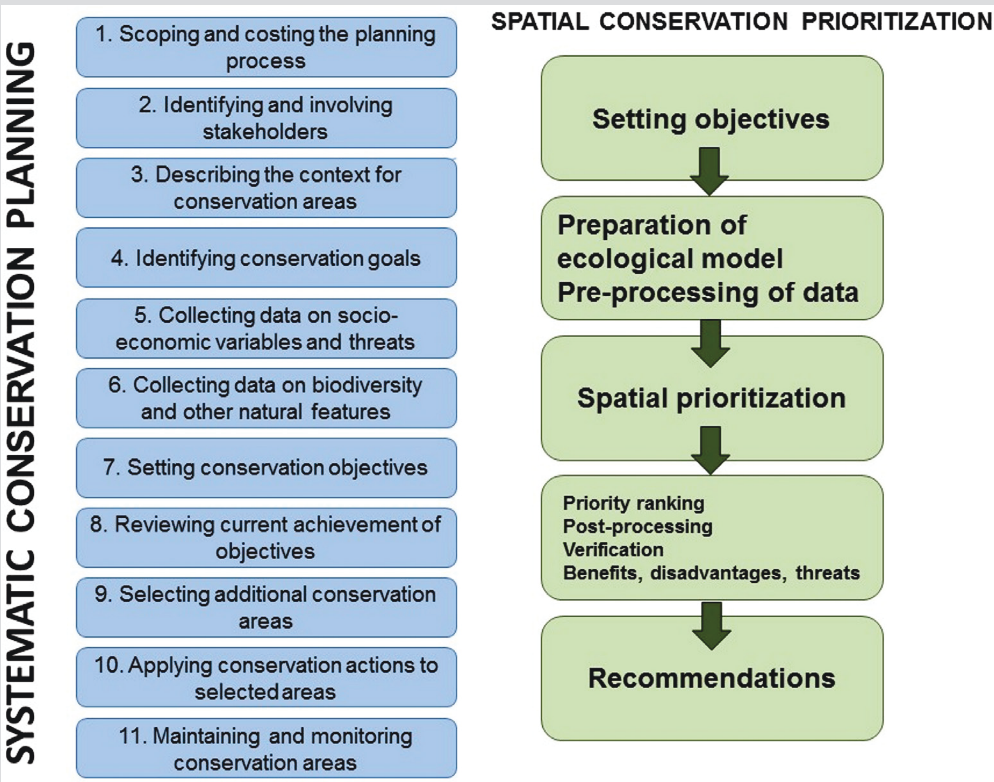
Many prioritization approaches have relied on different scoring methods, evaluating candidate sites individually or independently from each other based on various criteria (Moilanen et al. 2009). However, the pitfalls of *ad-hoc* and scoring-based site selection have become acknowledged and it has become apparent that prioritization methods solely accounting for species richness or rarity as indicators of conservation value are not always sufficient (Margules and Sarkar, 2007; Kullberg et al. 2015). This is because prioritizing only the most species rich areas does not necessarily capture the full range of the biodiversity (i.e. complementarity). In contrast, when proposed sites are assessed jointly as a set, accounting for the similarity of features in the sites, the resulting PA networks may be ecologically more efficient (Vane-Wright et al. 1991).

2.1.1.2 Spatial conservation prioritization and the problem of identifying an optimal protected area network

Systematic conservation planning, a special branch of conservation biology, evolved in the early 1990s with the aim of directing limited conservation resources in the most efficient manner in order to capture and ensure the persistence for most of biodiversity (Margules and Pressey, 2000). It has developed into a multidisciplinary science, employing and mixing methodology and ingredients from many other fields of science (Reyers et al. 2010). Systematic conservation planning includes identification of conservation goals, which may address a broader conservation vision, but then gets refined into qualitative or quantitative goals about biodiversity (e.g. representation) (Pressey and Bottrill, 2009; Box 1). Within the framework of systematic conservation planning, a spatial part

BOX 1. Systematic conservation planning framework and spatial conservation prioritization: the process view

The framework for systematic conservation planning adopted from Pressey and Bottrill (2009) and a simplified workflow for spatial conservation prioritization (SCP) process (adopted from Lehtomäki and Moilanen, 2013). The original systematic conservation planning approach had two broad objectives: to represent the full spectrum of biodiversity and ensure the long-term persistence of biodiversity in a set of conservation areas (Margules and Pressey, 2000). Within the context of systematic conservation planning, there is a data-driven operational analysis called spatial conservation prioritization or conservation assessment, which is used for identifying important areas for biodiversity. Principles and concepts addressing high-level conservation goals (e.g. mitigating species loss and extinction) are translated into preferably quantitative, lower-level objectives for operational use in SCP (Ferrier and Wintle 2009). These include, for example, complementarity and representativeness of a given PA network (Wilson et al. 2009). In other words, SCP allows identification of the contributions of existing PAs to conservation goals and provide the means for measuring the conservation value of different areas (Margules and Pressey, 2000).



of the process, spatial conservation prioritization (SCP), developed (Box 1). The original use of SCP has been to seek spatially explicit options for the preservation of biodiversity (Margules and Pressey, 2000; Sarkar and Illoldi-Rangel, 2010). It is important to note that there are a number of other (non-spatial) approaches for conservation planning, such as strategic conservation planning and conservation evidence (Groves and Game 2016), but they are not dealt with in this thesis.

In mathematical terms, a SCP problem can be interpreted as an optimization problem: findin the "best possible" conservation area network satisfying multiple conservation principles (Pressey et al. 1996; Sarkar et al. 2006; Moilanen et al. 2009). In the early years of systematic conservation planning the optimization process was come to be called as reserve selection or reserve network design (Margules and Pressey, 2000). Decision-theoretic optimization methods (so-called reserve or site selection algorithms; Csuti et al., 1997; Pressey et al., 1996; 1997) are applied in different software such as Marxan (Ball and Possingham, 2000), ConsNet (Ciarleglio et al. 2009), C-Plan (Pressey et al., 2009) and Zonation (Moilanen et al. 2005; 2014). Overall, the conservation planning problem can adopt a variety of formulations in terms of optimization and cost-efficiency is frequently associated with the process (Sarkar et al. 2006). The target-oriented model of specifying quantitative feature-specific objectives based on ecological thresholds and trying to satisfy them efficiently (i.e. target-based planning) has been widely adopted (Nicholson and Possingham, 2006; Carwardine et al., 2009). Common criticism towards target-based planning include that feature-specific targets may be set arbitrarily (Svancara et al. 2005) and there is a risk that that too many resources may be eventually used on individual features that occur in otherwise feature-poor areas (Di Minin and Moilanen, 2012). That said, SCP can be done without specifying targets for individual features (Moilanen et al. 2009; Di Minin and Moilanen, 2012). The Zonation software (Moilanen et al. 2005; 2014), which is extensively utilized in this thesis, is based on maximum-utility planning. In other words, Zonation aims at maximizing the retention of all biodiversity features by producing a complementarity-based and balanced ranking of conservation priority over the entire landscape. Zonation is also applicable to analysis with multiple types of spatial data about species distributions, such as abundance data (Moilanen et al. 2014), while other SCP software can take only presence-absence data as input.

To date, SCP tools are well-established and widely used in numerous conservation planning cases world-wide (Ferrier and Wintle 2009). The majority of recent SCP research is related to existing PAs at local to global scales (Rodrigues et al. 2004b; Brooks et al. 2006; Gaston et al. 2006; Lehtomäki et al. 2009; Butchart et al. 2012; Kullberg and Moilanen, 2014; Pouzols et al. 2014), providing insights on how effectively PAs represent the biodiversity of selected taxa and habitats. Whilst PA networks seem to perform ecologically better than random, previous evidence indicates that they may not be optimal (Rodrigues et al. 2004b; Bladt et al., 2009; Kark et al., 2015; Mazor et al., 2013; Pouzols et al., 2014) and little is still known about the connectivity of the present PA systems (Juffe-Bignoli et al. 2014). Furthermore, interest in measuring PA effectiveness as conservation impact has grown, creating new methods such as the counterfactual approach emphasizing effectiveness in reducing threats (Andam et al. 2008).

It is important to note that SCP is not only about identifying and assessing PA networks. The field has expanded its scope, for instance to identifying locations for phylogenetic diversity or genetic diversity (Taberlet et al. 2012; Pollock et al. 2015; Arponen and Zupan, 2016), restoring degraded habitats, or targeting impact avoidance (Kareksela et al. 2013; Moilanen, 2013; Kujala et al. 2015; Nin et al. 2016). Recently, Zonation has been used in the identification of green infrastructures in southern Finland (Kuusterä et al. 2015), bringing SCP closer to general land use planning. Despite some case studies, SCP is not yet a well-established component in general land use planning (Gordon et al. 2009). Given that the mission of PAs has expanded from biodiversity conservation to improving human welfare (Naughton-Treves et al. 2005; Oldekop et al. 2015), SCP has also increasingly employed socio-political considerations (Knight et al. 2006; 2011). Albeit being an important theme, it is not discussed in this thesis.

2.1.1.3 Ecosystem services as a new component in conservation science

Recently, ecosystem services (ES) have been seen as a new strategy for conservation, emphasizing biodiversity as a necessity for human prosperity and survival (Ehrlich and Ehrlich, 1981; Daily, 1997; Costanza et al. 1997). The origin of the concept of ES, "the benefits that humans obtain from ecosystems", can be traced back to the 1970s (Haines-Young and Potschin, 2009). Later, the Millennium Ecosystem Assessment (MA, 2005) has grouped ES into four categories: (1) provisioning services, such as food, water, and timber, (2) regulating services that affect climate, wastes, floods and water quality, (3) cultural services that provide recreational, aesthetic, and spiritual benefits and, (4) supporting services such as soil formation and nutrient cycling. While there are multiple definitions and classifications of ES (Saarikoski et al. 2015), CICES (2016) provides the most well-known and widely used classification of ES.

A common hypothesis assumes that ES will broaden the biodiversity conservation approach because ES themselves are an important part of ecosystem functioning (Kremen, 2005; 2007; Chan et al. 2007; Goldman et al. 2008). The ecosystem services cascade model connects ecosystems to human wellbeing and makes a distinction between ecological structures and processes and the benefits that people derive (Haines-Young and Potschin, 2009; Maes et al. 2012a). Hence, ecosystem processes, structure and composition only describe the provision of ES, and they become ES when there is a demand for the service (Chan et al. 2006; Fisher et al. 2009). Frequently, ES provision and demand have been described as flows which can be local, regional, or global (Fisher et al. 2009; Villamagna et al. 2013; Cimon-Morin et al. 2014; Serna-Chavez et al. 2014). The demand links ES closely to socio-economic importance and valuation of ES. There is a vast "natural capital" literature on monetary valuing and payments schemes around ES (see e.g. Gomez-Baggethun et al. 2010 for a starting point), which will not be discussed in this thesis. Some conservationists have raised concerns that the anthropocentric approach around ES, linking to the ideas of "new conservation" (Soule, 2013), distracts conservation from its original mission – protecting biodiversity based on its intrinsic value (Reyers et al. 2012; Schröter et al. 2014b). Hence, it may be difficult to find the common ground for biodiversity and ES in terms of conservation and landscape planning (Chan et al. 2007; de Groot et al. 2010; Reyers et al. 2012) due to the variety in ES definitions and applications. Despite increasing research, ES can be seen as a relatively diverse and contested concept (Schröter et al. 2014b) that is lacking consistent methodology (Seppelt et al. 2011).

An increasing amount of research has focused on understanding relationships between multiple ES and found that they may incorporate synergies and trade-offs (Bennett et al. 2009; Haase et al. 2012; Mace et al. 2012; Maes et al. 2012b; Seppelt et al. 2013). It is widely known that some ES are directly or indirectly dependent on ecological processes (Luck et al. 2003; Kremen et al. 2007) and that biodiversity has synergetic implications on some ES (Balvanera et al. 2006; Bennett et al. 2009; Whittingham 2011). These relationships and their spatial patterns have been extensively studied during the past decade. Naidoo et al. (2008) showed that regions selected to maximize biodiversity provide no more ES than regions chosen randomly. Nevertheless, some studies have found a more positive spatial coincidence (Cimon-Morin et al. 2013), but despite extensive research, (Chan et al. 2006; Costanza et al. 2007; Anderson et al. 2009; Mace et al. 2012; Reyers et al. 2012) gaps in knowledge still exist. Evidence is also mixed about how effectively existing PAs conserve ES (Pyke, 2007; Juffe-Bignoli et al. 2014; Eastwood et al. 2016).

SCP has also increasingly started to incorporate ES alongside biodiversity (Egoh et al. 2007; Luck et al. 2012; Cimon-Morin et al. 2013; Schröter et al. 2014a; Snäll et al. 2016). Moreover, common SCP concepts, such as complementarity, are starting to appear in ES studies (Cimon-Morin et al. 2016b). While the number of studies investigating spatial prioritization of ES has increased substantially, most of these have focused on one or a few ES (Chan et al. 2011; Orsi et al. 2011; Izquierdo and Clark, 2012; Thomas et al. 2013; Casalegno et al. 2014; Durán et al. 2014; Schröter et al. 2014a; Nin et al. 2016). Recently, the debate whether biodiversity and ES should be kept as conceptually distinct conservation targets has found its way also into SCP (Chan et al. 2011; Manhaes et al. 2016). Some ES have been described as "conservation compatible" meaning that the presence of the service could be regarded as an additional argument for conservation (Chan et al. 2011; Schröter and Remme 2016). Indeed, it has been recently shown that including ES to cost-effectively expand conservation networks can simultaneously encourage biodiversity conservation (Remme and Schröter, 2016). Inevitably, simultaneous spatial prioritization of multiple biodiversity and ES features entail trade-offs, and therefore true "win-win" solutions for both may be difficult to realize (McShane et al. 2011). Trade-offs are likely to occur for example between biodiversity and some provisioning services, such as extensive agriculture or timber harvesting. Furthermore, only a few studies so far have considered the methodological aspects of spatial prioritization of ES in any SCP software (Cimon-Morin et al. 2014; Schröter and Remme 2016; Snäll et al. 2016). Some have found that priorities may shift drastically when ES demand is taken into account (Chan et al. 2011; Cimon-Morin et al. 2016a). Nevertheless, none of the previous studies have been specifi on different ways of treating synergies and trade-offs, demand, flo , and connectivity in spatial prioritization. Overall, it seems that there are important differences when prioritizing areas for ES compared to biodiversity (Luck et al. 2012), and these matters clearly require further investigation.

2.1.1.4 Spatial conservation prioritization as spatially explicit exercise

Identifying spatial priorities for biodiversity and ES is a data-hungry exercise, and therefore SCP is constantly dependent on spatial data (Kullberg and Moilanen, 2014; Kendall et al. 2015). While explicit spatial information on all biodiversity cannot be obtained, SCP extensively utilizes surrogates, or features of the landscape such as species distributions or habitat types (Sarkar and Margules, 2002; Margules and Sarkar, 2007). In addition to biodiversity features, SCP may incorporate a wide range of other spatial data such as land uses, administrative regions, costs, and threats (Kullberg and Moilanen, 2014; Lehtomäki et al. 2016; Tulloch et al. 2016). However, despite a recent increase in spatial data resources, limited data still remains a true problem in SCP (Moilanen, 2012). A recent study by Joppa et al. (2016) also revealed how little data is actually available, at the global extent, about the spatial distribution of anthropogenic threats to biodiversity.

While funding for field surveys and monitoring is also limited, output maps based on species distribution modelling (SDM) have been increasingly used as input data in SCP (Fajardo et al. 2014; Tulloch et al. 2016). Originating from the late 1970s, SDM is a set of different quantitative methods for doing statistical inference about the drivers of species' distributions (Franklin, 1995; Thuiller et al. 2004; Elith et al. 2006). Multiple methods exist for modelling species' response to environmental gradients and to estimate species' range loss and gain (Guisan and Thuiller, 2005). SDMs have become important tools in conservation as they can be used to identify suitable environmental conditions across large geographic extents and due to their potential of guiding future survey efforts (Peterman et al. 2013). However, predicted species distributions always include some errors, e.g. false predictions that a species is absent (omission error) or present (commission error) (Elith and Leathwick, 2009). Overall, spatial priorities are sensitive to choice of biodiversity surrogates and types of SDMs (Lentini and Wintle, 2015).

Because ecosystems are heterogeneous and the provision of ES varies across space, ES mapping turns out to be a spatially explicit process. Geographic information systems (GIS) provide a useful tool for mapping, visualizing and analyzing ES provision (Burkhard et al. 2009; Potschin and Haines-Young, 2011; Tolvanen et al. 2014; Andrew et al. 2015). There are multiple GIS-based tools available for ES modelling and mapping, such as Co$ting Nature (Mulligan et al. 2010) and InVEST (Natural Capital Project, 2016), possibly being the most widely used web-based tool for mapping ES (Nelson and Daily, 2010). In turn, for the benefits-transfer or value-transfer approach for ES, an open-source GIS application ARIES may be a suitable tool (Villa et al. 2014).

While there are differences in how ES provision is translated into maps of service use, modelling ES provision from ecological production functions is the approach usually seen to be most applicable to decision support, as it allows predictions of how land use and management decisions might affect ES (Nemec and Raudsepp-Hearne, 2013). Overall, land cover and land use explain a considerable part of the variation in the spatial supply of ES (Maes et al. 2012a) and therefore most of the recent efforts to map ES provision have utilized different kinds of land use classifications (Burkhard et al. 2009; Haase et al. 2012; Kopperoinen et al. 2014). However, the capacity of a land use type to provide ES very much depends on the geophysical and socio-economic context as well as on the landscape structure (Stürck and Verburg, 2016). GIS is a suitable tool for mapping the spatial distribution of community values and threats for ES (Raymond et al. 2009). Yet, the need to account for spatial variation in ES demand (human beneficiaries) has been recognized and received increased attention (Hein et al. 2006; Burkhard et al. 2012; Bagstad et al. 2013; Cimon-Morin et al. 2014). However, there is still varying understanding of the concept of ES demand, which has fundamental implications on how and where ES demand is being mapped (Wolff et al. 2015). Hence, a clear distinction between ES capacity, flow and demand could improve operationalization of ES mapping (Baro et al. 2016). Despite the rapid development in the field of ES mapping, there is still considerable inconsistency in methods to quantify ES, which challenges their inclusion into policies and natural resource management (Crossman et al. 2013).

2.2 POLICY FRAMEWORK

2.2.1 THE EUROPEAN UNION'S POLICY SAFEGUARDING EUROPEAN BIODIVERSITY AND ECOSYSTEM SERVICES

The European Union has been active in building policy tools for mitigating biodiversity loss. While the EU has experienced expansion in the past decades, from 15 to 28 Member States, conservation policies have simultaneously shifted towards a continental scale approach (Cogalniceanu and Cogalniceanu, 2010; Evans, 2012; Born et al. 2015). The EU biodiversity strategy includes the Birds and the Habitats Directives, which represent the cornerstones of the EU biodiversity policy (EC, 2011a, b). The legislation in the Directives require designation of sites to the EU-wide network of PAs, the Natura 2000 network (N2k), bringing policy closer to the themes in SCP. In simple terms, conservation policy can be defined as institutionalized behaviors or practices that affect conservation activities (Game et al. 2015). Establishment of the N2k is an area-based example of these institutionalized practices. Policies can be described as either policy-driven or evidence-based, according to how much they are based on scientific grounds (Svancara et al. 2005). While the EU has recognized the intrinsic value of nature conservation, it has also adopted the ES approach for the first time in the EU biodiversity strategy to 2020 (EC, 2011a). The area-based conservation policy schemes around the EU biodiversity strategy are introduced in detail in Box 2. The EU states that the protection of both biodiversity and ES is crucial for social and economic well-being, coherence and competitiveness in the EU (EC, 2011a). Therefore, the Commission contributes yearly to nature conservation under its own LIFE funding scheme. For example, during the 2014-2020 funding period, the EC will contribute approximately €3.4 billion to the protection of the environment and climate (EC, 2016a).

2.2.1.1 Area-based conservation in continental policy and legislation: the Nature Directives and the Natura 2000 network of protected areas in the European Union

The most common exercise in SCP has been identifying PA networks. The EU has also conducted such a spatial conservation planning exercise at the continental scale. The EU efforts to conserve biodiversity have been consistently directed towards the protection of targeted habitats and species through the designation of PAs under the Birds Directive (EC, 2014a) and the Habitats Directive (EC, 2014b). In practice, this activity has been made operational through the establishment of the EU's own ecological network of PAs: the Natura 2000 network (N2k). At every turn, the N2k and the two directives are highlighted as the main tools of the EU's biodiversity strategy (EC, 2011a).

Currently, the N2k network consists of more than 27 000 sites of different size, covering approximately 18% of the EU's land area (EEA 2012; EC, 2016b). Overall, the N2K has experienced significant expansions during the past ten years due to the addition of new EU Member States. As a result, there are some Member States with large areas (>20% of land) covered by the N2k network while others have relatively low coverage (EC, 2013c; 2016b). While the number of PAs in Europe is high, their average size is quite small, reflecting the fact that the EU land area is highly fragmented. In addition to the continental extent, the N2k is an exceptional PA network due to the fact that all of its area is not strictly protected (Evans, 2012). The term "protected area" covers a variety of designations given to parcels of land, ranging from national parks and strict reserves to different types of management areas (EEA, 2012; Born et al. 2015). Indeed, some areas allow agricultural or other land use activities. In addition, some Member States also have their own area-based conservation schemes, such as nationally designated PA networks, with some of them overlapping the N2k (EEA, 2013). The diversity and complementarity of different PA designations reflect the history, administrative realities, and commitments to nature conservation of each Member State. In total, 25.6 % of the EU's terrestrial land is recently protected under N2k or national designations or a combination of these two (EEA, 2013).

The N2k consists of two types of sites designated on the basis of the Birds Directive (79/409/EEC) and the Habitats Directive (92/43/EEC). As being the oldest tool of the EU biodiversity policy, launched in 1979, the Birds Directive includes two main conservation obligations. The first obligation was to create a network of Special Protection Areas (SPAs) for targeted bird species. Second, there is a requirement for direct protection of species through interdictions of killing, taking, disturbing wild birds, and strict regulation of hunting and trade (EC, 2014a). The Habitats Directive was the second major legal instrument launched in 1992, moving the focus from species-based conservation to habitats and introduced the concept of favorable conservation status. The Habitats Directive aims to select Sites of Community Interest (SCIs) for target species and habitats (EC, 2014b). Target species are listed in the Annexes of these two Directives (EIONET, 2014a, 2014b). The full implementation of the Directives is listed as Target 1 in the biodiversity strategy (EC, 2011a).

2.2.1.2 Site selection process of the Natura 2000 network

The EU's aim of the Natura 2000 network (N2k) to protect biodiversity "irrespective of national or political boundaries" clearly implies that site designation should be developed under EU-level criteria and coordinated planning (EC, 2009). The selection of Sites of Community Interest (SCIs) for species and habitats listed in the Habitats Directive (EIONET, 2014a) is a cooperative process between the Member States and the Commission (EC, 2014b). In contrast, Special Protection Areas (SPAs) for birds listed in the Birds Directive are selected by the Member States with no commonly agreed EU-wide criteria (Evans, 2012; Gruber et al. 2012). From the perspective of systematic conservation planning, this site selection process has often been criticized as non-systematic and lacking of clear quantitative criteria (Gaston et al. 2008; Apostolopoulou and Pantis, 2009; Giakoumi et al. 2012; Kati et al. 2015).

While the sites classified by Member States under the Birds Directive (SPAs) are semi-automatically included in the N2k, sites designated under the Habitats Directive follow a unique multi-step process before they can be included in the network (Evans, 2012; EC, 2014b; EC, 2016c). At the first stage, preliminary sites are identified and proposed by the Member States based on criteria set in the Directive. Secondly, the European Commission assesses, by each biogeographical region, the sufficiency of these sites for each target species and habitat type (EC, 2016c). Second, the EU-level importance of each site is evaluated according to the criteria set in the Directive, and the Commission adopts and publishes a list of Sites of Community Importance (SCIs) for each biogeographic region. Ultimately, the Member States categorize the SCIs as Special Areas of Conservation (SACs) after adoption of the required legal and administrative measures necessary for their management (EC, 2009).

The application of the biogeographical regions approach in the SCI site selection emphasizes the fact that the EU recognize the ecological conditions and differences within and between the

BOX 2: The European Union's biodiversity strategy to 2020: an overview of area-based conservation targets

In spring 2011, the EU adopted a new strategy to halt biodiversity loss in the EU by 2020, aiming at improving the state of Europe's species, habitats, ecosystems, and ES. The EU biodiversity strategy includes six measurable targets with sets of actions. For instance, these actions include full implementation of existing EU nature legislation, including the Birds and Habitats Directives and the implementation of the N2k network (Target 1). Moreover, the strategy is closely linked (Target 6) to global biodiversity targets and in line with the commitments made by the EU in the global conference of the Convention on Biological Diversity (CBD) in Nagoya, Japan, in 2010 (EC, 2011a). The related area-based target 11, states that "*By 2020, at least 17 per cent of terrestrial and inland water, and 10 per cent of coastal and marine areas, especially areas of particular importance for biodiversity and ecosystem services, are conserved through effectively and equitably managed, ecologically representative and well connected systems of protected areas and other effective area-based conservation measures, and integrated into the wider landscapes and seascapes*." Besides the Aichi target 11, the second political mandate which led to the adoption of the new EU biodiversity strategy initiated from the EU Member States' conclusion that the previous biodiversity policy was not achieving its targets (EC, 2011b).

In addition to Target 1 in the EU Biodiversity Strategy, which is central for area-based conservation, there are other area-based conservation objectives in the strategy. For instance, the specific target for restoring 15% of degraded ecosystems and establishing Green Infrastructure (Target 2) connects strongly to area-based conservation. Moreover, the EU's own Green Infrastructure (GI) strategy distinguishes the need for implementing interconnected green infrastructures (EC, 2013a). That said, as PAs can be seen as core elements of GI, the aim is to improve the connectivity of the core areas of the EU's green infrastructure (the N2k), but also to facilitate maintenance of ES in the EU (Maes et al. 2015a). It is often argued that the Birds and the Habitats Directives cannot achieve the nature conservation targets alone (Born et al. 2015). Thus, the EU biodiversity strategy incorporates other biodiversity objectives, which do not necessarily contribute explicitly to any area-based targets. These include for example sectoral policies such as the Common Agricultural Policy and Common Fisheries Policy and the Water Framework Directive (EEA, 2012). While the EU has several policy agendas, joint legislation, and actions for protecting the EU-wide biodiversity and ES, continuous evidence is needed about their effectiveness. In February 2014, the European Commission received a mandate to deliver a "Fitness Check" of the Birds and Habitats Directives as part of the Commission's Regulatory Fitness and Performance program (REFIT), aiming at simplifying EU law (EC, 2014c). This exercise, nearing its completion, confirmed the need to assess the effectiveness, efficienc , relevance, coherence, and the EU added value in the implementation of the Birds and the Habitats Directives.

Given the potential to motivate people to protect biodiversity, the concept of ES has been appealing to the EU policy-makers. Thus, ES are for the first time clearly addressed in the EU biodiversity strategy to 2020: "*Conserving biodiversity is not just about protecting species and habitats for their own sake. It is also about maintaining nature's capacity to deliver the goods and services that we all need, and whose loss comes at a high price*." Action 5 (as part of Target 2) of the biodiversity strategy requires Member States to map and assess the state of ecosystems and their services in their national territory with the assistance of the European Commission (EC, 2011a). Hence, the EU has initiated related policies in the context of MAES process (Mapping and Assessment of Ecosystem Services), the objective of which is to support the implementation of Action 5 (EC, 2013b; Maes et al. 2012a; Maes et al. 2016). In line with the Millennium Ecosystem Assessment, the target of the EU's own assessment is to provide a critical evaluation of the best available information for guiding decisions about ES. The paper proposes a detailed typology of ecosystems to be assessed and mapped by using the Common International Classifi ation of Ecosystem Services (CICES, 2016), originally developed for environmental accounting purposes. Despite Aichi target 11 (CBD, 2016) mentioning ES, there are no clear area-based targets or direct requirements to set aside areas specifically for ES conservation in the EU. Nevertheless, actions proposed in relation to Target 2 strongly emphasize mapping and assessment of the biophysical potential of ES, whilst considerations for ES demand do not yet exist (Maes et al. 2012a; 2016).

GLOBAL

The Convention on Biological Diversity (Aichi Targets)
5 strategic goals, 20 specific targets
Adopted in Nagoya, Japan, 2010

Target 11: at least 17 per cent of terrestrial and inland water, and 10 per cent of coastal and marine areas, especially areas of particular importance for biodiversity and ecosystem services should be conserved

EUROPEAN UNION

The EU Biodiversity Strategy to 2020
6 measurable targets with sets of actions
Adopted in May, 2011

TARGET 1. Fully implement the Birds and Habitats Directives: requirement for Member States to designate and manage core areas for conservation - the Natura 2000 network

TARGET 2. Maintain and restore ecosystems and their services: promoting a European green infrastructure
Action 5: Improve knowledge of ecosystems and their services in the EU

TARGET 3. Increase the contribution of agriculture and forestry to biodiversity

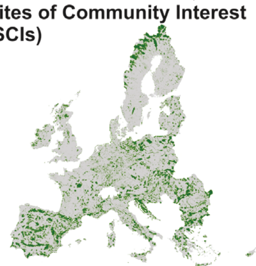
TARGET 4. Ensure the sustainable use of fisheries resources

TARGET 5. Combat Invasive Alien Species

TARGET 6. Step-up action to tackle the global biodiversity crisis: the EU's contribution to global biodiversity conservation - 17% target

The Birds Directive, 1979
Special Protection Areas (SPAs)

The Habitats Directive, 1992
Sites of Community Interest (SCIs)



The Natura 2000 network

The EU Green Infrastructure Strategy: "need to develop, preserve and enhance healthy green infrastructure to help stop the loss of biodiversity and enable ecosystems to deliver their many services to people and nature. The greater the scale, coherence and connectivity of the green infrastructure network, the greater its benefits."

MEMBER STATES

Implementation of the strategies and targets
Site selection and designation

Member States and hopes that the site designation process would be based on scientific data. The biogeographical regions (EEA, 2014a; EC, 2016c) have been used to design the network but also to identify target species and habitats. To date, the EU has classified the region to nine biogeographic regions: Alpine, Atlantic, Black Sea, Boreal, Continental, Macaronesian, Mediterranean, Pannonian, and Steppic (EC, 2016c). The idea of identifying relevant sites across borders better takes into account the natural distribution of species and habitats. Building a PA network across the EU relying on a common methodology and ecological criteria helps achieve better ecological coherence than if the networks were decided independently within each Member State. Thus, the ultimate aim of the N2k is to protect species and habitats across the entire EU and paying special attention to migratory species, genetic diversity, and ecological variability of the region (EC, 2009).

2.2.1.3 Extensively studied, moderately known: previous research assessing the Natura 2000 network

The Natura 2000 network (N2k) has attracted major research interest and hundreds of academic research papers and policy reports have explored the network from both ecological and socio-political perspectives (Popescu et al. 2014; Blicharska et al. 2016; Orlikowska et al. 2016). A number of previous research studies have demonstrated the ecological effectiveness of the terrestrial Natura 2000 network (Gruber et al. 2012). Many have also found the SPAs useful in conserving wild birds in the EU (Donald et al. 2007; Devictor et al. 2007; Pellissier et al. 2013; Kolecek et al. 2014; Sanderson et al. 2015; Beresford et al. 2016). Nevertheless, other studies have found the current N2k insufficient to conserve particular species or habitats and the effectiveness of the network is not yet comprehensively understood (Lopez-Lopez et al. 2007; Albuquerque et al., 2013; Bagella et al., 2013; Mikkonen and Moilanen, 2013; Petersen et al. 2016).

While many existing N2k assessments are taxonomically and geographically biased (Orlikowska et al. 2016), key research themes have been ranging from quantitative empirical studies and ecological gap analyses (Maiorano et al. 2007; Jantke et al. 2011; Abellán et al. 2015) to evaluations on network connectivity (Opermanis et al. 2012) and climate change adaptation (Araújo et al. 2011; Thuiller et al. 2015). While some researchers have examined the policy change, implementation, and the site selection process (Evans, 2012; Kati et al. 2015; Borrass et al. 2015; Romao, 2015), some have found varying local attitudes in the Member States towards site designations (Hiedanpää, 2002; Sorgo et al. 2016). Multiple stakeholders, scientists, and policy-makers have recently considered the overall added value of the N2k (EC, 2014c; Romao, 2015). Orlikowska et al. (2016) reviewed the most important ecological knowledge gaps in terms of N2k. They found that there is a need for new studies encompassing large spatial scales and focusing on underrepresented taxonomic groups such as reptiles and amphibians. Hence, this thesis focusing on EU-wide spatial assessments with a representative set of vertebrate species may serve as a source for filling these knowledge gaps.

3. MATERIAL AND METHODS

3.1 STUDY AREA

This thesis is composed of two conceptual chapters (Chapters I and II) and three case studies (III, IV and V) within the EU (Figure 2). The EU and its 28 Member States are characterized by a great diversity of landscapes, spanning 9 biogeographic regions (EEA, 2012; EC, 2016c) each of which reflect special climatic and geological conditions. Consequently, biodiversity varies significantl across the region and includes one global biodiversity hot spot, the Mediterranean area, which is home for over 20 000 endemic vascular plant species (CI, 2005). However, recent data by EEA (2016) shows that 60% of species assessments and 77% of habitat assessments continue to find an unfavorable conservation status.

In terms of land use, Europe is one of the most fragmented continents in the world (Gaston et al. 2008; EEA, 2012). In particular, landscapes in central Europe have undergone rapid change through urbanization, agricultural intensific tion, forestry, and development of transport infrastructure (Gerard et al. 2010; Born et al. 2015). Almost half of the land in the EU is used for agriculture, making this sector a major land use element across the region (EC, 2011b). Recently, agricultural land abandonment is a process that extensively influences the landscape (Navarro and Pereira, 2012; Plieninger et al. 2016). The density of the human population in Europe is another factor explaining landscape patterns. While the present population size of the EU is 508 million in total (Eurostat, 2016b), the highest population density is found in the coastal regions, whereas the lowest population densities are in the northern parts of the EU. Hence, wilderness areas mostly remain at certain high-latitude or high-altitude areas, e.g. in some parts of Fennoscandia and the mountain ranges of central and southern Europe. In general, the biogeographical diversity and history of human intervention explains the relatively large number of PAs in the EU but also their relatively small size compared to PAs elsewhere in the world (EEA, 2012).

Overall, the EU provides an interesting context and case study setting to investigate the potential of continent-wide conservation using spatial conservation prioritization tools. The EU has been seen as a forerunner in nature conservation as it has its own large-scale PA network. Second, the EU provides a unique setting from an administrative perspective because of the common policy and legislation to protect biodiversity and ES (EC, 2009). Third, spatial data availability on species distributions and environmental datasets is relatively good. Nevertheless, the majority of studies that have investigated the N2k using SCP methods have been conducted at a national scale or focused on other taxa than in this thesis (e.g. Jantke et al. 2011; Mikkonen and Moilanen, 2013).

3.2 DATA

This thesis extensively utilizes spatial conservation prioritization methods and therefore the main data used are spatial (map) data sets. The following sections and Table 1 give an overview of the main data sources and methods used in this thesis. Detailed descriptions of the data and methods can be found in the respective Chapters (I-V).

This thesis mostly utilized openly available spatial data resources, such as data by the European Environment Agency. Some proprietary data was used as well, including the species distribution

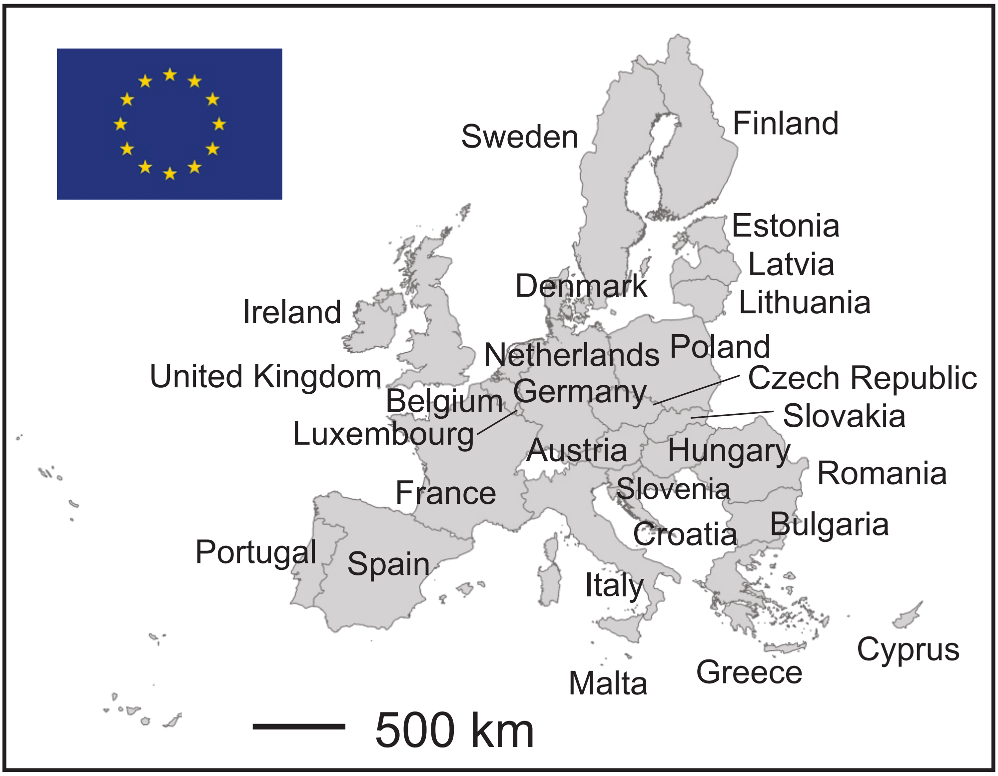


Figure 2. The European Union and the 28 Member States.

data used (Maiorano et al. 2013). The data on Important Bird and Biodiversity Areas was provided upon request by BirdLife International (2015).

3.2.1 Literature review

In order to conduct the review for Chapter I, I collated comprehensive literature about systematic conservation planning, SCP, and other relevant topics related to spatial allocation of conservation effort. I searched for citations from Thomson Reuters' Web of Science by using a targeted search and retrieved article full texts within the limits of the library access permissions of the University of Helsinki. Next, a full text search was applied using the Adobe Acrobat X and PowerGREP tools (Powergrep, 2011). Every mention of the core terms inside the PDFs was investigated. Thus, a fairly broad literature base was searched thoroughly and literature chains were followed outside the basic set. As there were some older articles and books not available in electronic form, I investigated them manually. Known prior summaries into spatial conservation prioritization were also included as starting points (e.g. Margules and Pressey, 2000; Justus and Sarkar, 2002; Sarkar et al. 2006).

Chapter II utilizes extensive literature on ecosystem services science and SCP. For Chapters III, IV and V, I went through an extensive set of recent EU policy documents about area-based biodiversity conservation and related legislation. Most of these reports were downloaded from the European Commission's websites.

Table 1. List of datasets used in this thesis and in which individual chapter they were used.

Species distribution data			
The vertebrate species data used as input for spatial prioritization were species-specific expert-based distribution models over the Western Palearctic. Known ecological habitat requirements were used to refine species distributions via an expert-based modelling approach. Each pixel was classified as suitable habitat (1) or not (0).	1.5 km x 1.5 km	Maiorano et al. 2013 Further details about the data can be found also in Chapter III and IV.	III, IV
Species subsets: - The Birds directive species - The Habitats directive species (Annex II species and Annex IV species) - All Directive species - Species categorized according to IUCN status		Species lists were derived from EIONET code lists. EIONET, 2014a; 2014b IUCN, 2014; 2015	
Ecosystem services data			
We used four regulating and one cultural ES for both provision (capacity) and demand maps for the EU.	1 km x 1 km	Further details about the data can be found in Chapter V.	V
Air quality Carbon sequestration Flood control Pollination Urban leisure		Maes et al. 2015b Schulp et al. 2008 Stürck et al. 2014 Schulp et al. 2014 Based on land cover scores in combination with multiple additional variables.	
Protected areas and networks			
The Natura 2000 network and its subsets: - Terrestrial Special Protection Areas (SPAs) - Terrestrial Sites of Community Interest/ Importance (SCIs) - All terrestrial Natura 2000 sites	1.5 km x 1.5 km	EEA, 2014b	III, IV
Important Bird and Biodiversity Areas (European IBAs)	1.5 km x 1.5 km	BirdLife International, 2015	IV
Biogeographical regions European wide map of the 11 biogeographical regions independent of political boundaries, extracted to the EU extent (resulting in 9 biogeographical regions)	1.5 km x 1.5 km	EEA, 2014a	III
Administrative regions			
EU Member states: ArcGIS country polygons	1.5 km x 1.5 km	ESRI, 2011	III, IV
Exclusive Economic Zones (EEZ) (country polygons were refined by EEZs)	1.5 km x 1.5 km	Maritime Boundaries Geodatabase, version 6, VLIZ, 2012	III, IV
NUTS areas according to the NUTS classification (Nomenclature of territorial units for statistics is a hierarchical system for dividing up the economic territory of the EU).	1 km x 1 km	Eurostat, 2016a	V

3.2.2 Species data

The vertebrate species data used in Chapters III and IV as the input for spatial prioritization were species-specifi expert-based distribution models over the Western Palearctic. This data set was created and first introduced by Maiorano et al. (2013). Subsequently, these same distribution models have been used in multiple other studies (e.g. Maiorano et al. 2015; Thuiller et al. 2015). The species maps were cut to the EU extent, resulting in 841 maps for vertebrate species: 435 birds, 85 amphibians, 138 reptiles, and 179 mammals. I used multiple subsets of this data, categorized based on taxa, directive species status, and threat status (IUCN, 2014; 2015).

I did not use any separate land use data layers as the land use had been accounted for in habitat suitability scores when compiling the species distribution models (see Maiorano et al. 2013). Specificall , known ecological habitat requirements were used to refine species distributions via an expert-based modelling approach in order to produce a map for each species at 300 m resolution. There, each pixel was classifi d as suitable habitat (1) or not (0). The models went through a validation process using randomizations and known points of presence. For computational feasibility regarding the prioritizations done in Chapters III and IV, the datasets were aggregated to a 1.5 km resolution by summing the number of suitable 300 m pixels within each 1.5 km pixel, resulting in pixel suitability values between 0 and 25.

3.2.3 Ecosystem services data

Despite the fact that Chapter II extensively discusses ES data in SCP, no actual data on ES were used as the study was purely conceptual and methodological. However, in Chapter V, ES data played a key role. The data consisted of four regulating and one cultural ES for which both ES capacity and demand maps were available across the EU at a 1 km resolution. These five ES included global (carbon), regional (flood control), and local (pollination, air quality, and urban leisure) ES flow (Table 1). The landscape's capacity to provide each ES was mapped as was the fraction of ES capacity demanded by society. Thus, there were separate maps for ES provision capacity and ES demand. Chapter V focused on ES related to natural vegetation and excluded therefore urban and water land cover classes. Agricultural land was included only if hedgerows were present (van der Zanden et al. 2013). Detailed descriptions of the data and ES mapping are included in Chapter V.

3.2.4 Other spatial data and pre-processing

As Zonation can utilize only raster data as input, spatial analysis using Zonation sets special requirements for data pre-processing (Lehtomäki et al. 2016). To name a few, these include the same pixel size, extent, alignment, and coordinate system. These requirements were taken into account in all data manipulations in this thesis. In addition to species and ES data, I used several other data sets such as PAs and biogeographical regions (Table 1). Administrative regions data included country polygons and NUTS areas in the EU (ESRI, 2011; Eurostat, 2016a). Additionally, in Chapter IV, I used data provided by BirdLife International (2015) about Important Bird and Biodiversity Areas (IBAs).

When it comes to PAs, I rasterized the latest version of the terrestrial Natura 2000 network (EEA, 2014b). In addition, polygons of all terrestrial SPAs and SCIs were extracted because I analyzed birds and habitats directive species both separately and together. Likewise, the IBAs in the EU (BirdLife International, 2015) were rasterized into the same extent and resolution as the species data. All datasets were extracted and rasterized by using the cell center method in ArcGIS 10.2 (ESRI, 2015).

3.3 SPATIAL ANALYSES

3.3.1 Spatial conservation prioritizations using Zonation

In Chapters III, IV, and V, I used a quantitative GIS-based method for spatial prioritization and ecologically based land use planning: the Zonation software (Moilanen et al. 2005; 2014). Zonation is software for conservation and land-use planning, capable of doing data rich, large-scale, and high-resolution spatial analysis. Zonation differs from other SCP tools such as Marxan (Ball and Possingham, 2000), in which the typical aim is to achieve feature-specific targets with minimum cost (e.g. finding a spatial solution when species *x* retains 40% of its coverage). Instead of a target based solution, Zonation produces a priority ranking through the landscape, leading to a balanced priority ranking solution, while trying to maximize the retention of all features (Lehtomäki and Moilanen 2013). In Zonation, the conservation levels of features arise as emergent properties from general principles of aggregating conservation value across many biodiversity features, space, and time. There are great conceptual, technical, and practical differences between Zonation and other SCP software.

All spatial prioritizations in this thesis were carried out using Zonation version 4.0 (Moilanen et al. 2014). Zonation utilizes raster data and bases the prioritization on the distributions of biodiversity features (most commonly species) and optional data such as costs and land use restrictions. The quality of locations within the distribution of a feature can vary, modeled by variable suitability values given for each feature in each grid cell. Zonation is capable of accounting for feature-specifi and pair-wise connectivity (Moilanen et al. 2009) but can also retain corridors during the ranking (Pouzols and Moilanen, 2014). First Zonation accounts for the fraction of the occurrences of each feature in each pixel and then ranks pixels by iteratively removing the least valuable remaining cell until the complete landscape has been prioritized (Moilanen et al., 2005; Lehtomäki and Moilanen, 2013). When running the analysis, the program goes through all pixels and calculates the aggregate loss expected from the loss of each individual grid cell. Occurrence levels of features go down after the removal (ranking) of each grid cell and are tracked through the prioritization, influencing how valuable the remaining occurrences of each feature are seen. This process allows maintenance of a balance (~complementarity) through the full ranking, as features that have lost comparatively much rise in their importance.

While the Zonation algorithm is the same in all analyses, it has several conceptual options on how to calculate conservation value, i.e. so-called alternative cell removal rules define how conservation value would be aggregated across features and space. Across all prioritizations in Chapters III and IV, I used the core area method (CAZ; Moilanen et al., 2005, 2014), which bases ranking on the most important occurrence of a (biodiversity) feature in a grid cell, identifying high-priority areas that include high-quality locations for all features, even those that occur in otherwise feature-poor areas. In particular, CAZ is an appropriate method for spatial prioritization when data are available for all species of interest across the study area (Moilanen et al., 2005). This coincides well with the N2k target of retaining the best habitats and preserving all directive species (Chapter III and

IV). Prioritizations in Chapter V utilized the ABF method, additive benefit function, which has the heuristic interpretation of minimization of expected extinction rates via feature-specific species-area curves. It sums the loss across features, somewhat implicitly emphasizing pixels with many features in them, thereby giving slightly higher priority for generally more feature-rich areas than CAZ. This suits well with the aim of finding multifunctional ES priority areas. However, relatively feature-rich areas may be favored at the expense of some features occurring in feature-poor areas (e.g. some rare occurrences of ES in otherwise feature-poor areas). Overall, when developing the priority ranking in Zonation, concepts and principles such as connectivity, complementarity, and balance between features are accounted for.

There are multiple things to carefully consider before starting spatial prioritization analysis. Data and parameter selection is an important part of designing the ecological model of conservation value, implicitly aiming at accounting for the high-level conservation goals (e.g. mitigating species' extinctions) by choosing appropriate lower level objectives for prioritization (Lehtomäki and Moilanen, 2013). The SCP process in Zonation is described in detail by Lehtomäki and Moilanen (2013) and Lehtomäki et al. (2016).

3.3.2 Hierarchical prioritization and administrative unit analysis in Zonation

I applied a hierarchical prioritization in Zonation for analyses in Chapter III and IV. It is an analysis method that requires a mask raster file, often representing some existing PA network such as the N2k in this thesis. The mask raster file can indicate at least two hierarchical levels for prioritization (e.g. area within and outside N2k), but in some cases it may be useful to divide the landscape into multiple hierarchical levels. In hierarchical prioritization, all the pixels are first ranked from the surrounding area of the mask raster, and after that pixels are ranked in the order specified in the mask raster file (Moilanen et al. 2014). Generally speaking, this method allows for a gap analysis and examination of the coverage of species' ranges in a given network. At the same time, hierarchical analysis identifies the most efficient expansions of an existing PA network: these are the top-priority cells outside the PAs (e.g. N2k). These cells are the ones that most rapidly increase coverage of species distributions in the network. The EU Member States have committed through CBD Aichi Target 11 to protect at least 17% of their terrestrial and inland water areas, particularly those of importance for biodiversity, by 2020. Hence, in Chapter IV, I assessed the expansion of terrestrial SPAs from the current 12.5% to cover a theoretical 17% of the EU. A similar expansion analysis was conducted by Pouzols et al. (2014) to investigate the potential of expanding the global PA network.

Another essential method (Chapter III) was the administrative unit analysis function (ADMU) in Zonation (Moilanen and Arponen, 2011; Moilanen et al. 2014). This analysis also requires an additional raster file, now indicating a subdivision into administrative areas (such as Member States or biogeographical areas). I used the strong variant of administrative analysis (Moilanen and Arponen, 2011), which requires all features to be represented separately in each administrative region when possible. The strong variant is in contrast to the weak, which has different weights for features in different administrative areas, but which views distributions of features in the global context rather than in the context of each administrative area separately. Here, zero weight was given to the global component of administrative unit analysis, effectively meaning that an independent prioritization was done in one go for each Member State or biogeographical region in the EU. These alternative prioritizations allowed to imitate a process where conservation planning is either a pure group effort of the EU or where each country or biogeographical region is independently responsible for the allocation of sites. (And these alternative strategies for priority ranking can then of course be compared in terms of various measures of conservation performance.) Finally, to assess baseline representation levels, I also conducted randomized runs in Zonation, in which pixels are ranked randomly without any consideration of local occurrence levels of features.

3.4 INTERPRETATION OF THE RESULTS

3.4.1 Examining and visualizing spatial priority patterns

The first Zonation analysis output is a priority ranking map (Figure 3). Hence, the most essential results in this thesis were shown by maps (Chapters III, IV, and V). The output of a Zonation analysis is a raster file, representing the ranking of the landscape in terms of conservation priority. A unique priority rank value (from 0.0 to 1.0) is assigned to each individual pixel in the prioritization result map. In some cases, one could also use the second map output of Zonation, a wrscr.asc file, which contains a weighted range size rarity map. (This measure is similar to richness, but it accounts for the distribution size of each feature and the weight given to the feature.) In this case, no balanced priority ranking is done and range size rarity value of each cell can be used as a score-like measure of value for cells.

I analyzed spatial patterns by comparing pixel values in top priority areas across the EU. For example, mean and median pixel-specific priority ranks were calculated separately across each Member State or biogeographical region. Similar calculations were done also for the five ES in Chapter V, except regional units accounted for were either NUTS areas or ES flow zones. In Chapter III, I also compared pair-wise spatial overlaps between the top priority pixels in N2k against the same extent of top priority pixels (18.3%) in the three hypothetical optimal prioritizations (EU, Member State, and biogeographical regions). The top priority pixels for each prioritization were extracted from output maps of Zonation in ArcGIS. In order to evaluate the spatial configuratio of the N2k sites and how much top priority pixels were concentrated in border areas, I calculated Euclidean distances from each pixel in the N2k to the closest member state border. The same distance calculations were done also for the top priority pixels in the three hypothetical prioritizations (EU-wide, Member State, and biogeographical scenarios). Detailed descriptions of these calculations can be found in respective Chapters (III, IV, V).

3.4.2 Quantifying representation and efficiency

The second output of a Zonation analysis is a text file, called as curves.txt (Moilanen et al. 2014). I utilized the “performance curves” in order to explore how well certain areas (i.e. top *x*% of the priority ranking) cover the distributions of input features, such as vertebrate species or ES in this thesis. In other words, the curves report the remaining proportion of a feature’s range across all stages of the landscape ranking (Figure 3). The performance curves were examined for all prioritizations in Chapters III, IV, and V, and especially from hierarchical prioritizations for the N2k and its sub-networks and for IBAs. The curves directly reveal the proportion of species’ distributions inside a given percentage of landscape (i.e. within the top 18.3% of pixels and corresponding the extent of N2k, species *x* retains 27.3% of its total suitable habitat). In Chapters III and IV, network coverage

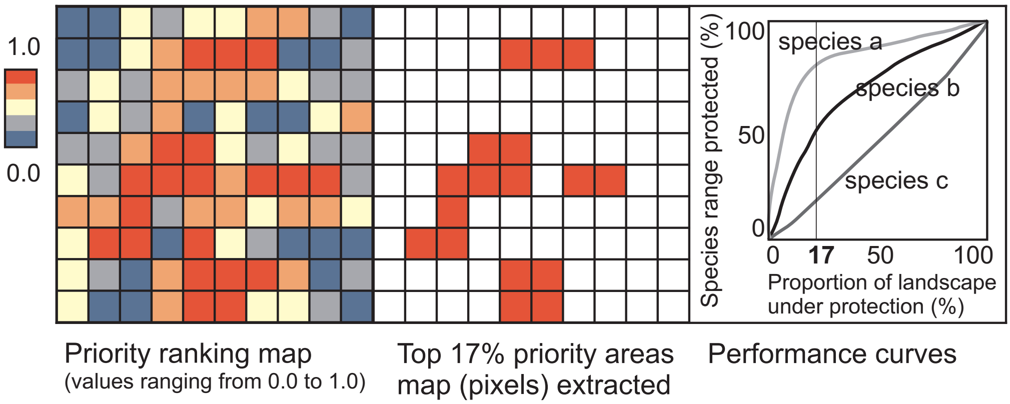


Figure 3. Simplified illustration of the Zonation outputs. The main Zonation output is a priority ranking map (in the left panel), representing the ranking of the landscape in terms of conservation priority (pixel values from 0.0 to 1.0). Pixels have been zoned to colors based on the priority rank, with highest priorities shown in red. The panel in the middle shows the top 17% priority areas extracted based on the priority ranking in the left panel. Performance curves are plotted (in the right panel) for three species (a, b, c) and they report the proportion of species' ranges at different stages of the landscape ranking. For example, when 17% of land is under protection, species b retains 50% of its habitat.

was compared between taxa, directive species status, and between species' threat status in different IUCN Red List categories (IUCN, 2015). In Chapter III, I evaluated vertebrate species coverage in N2k sites against four same-sized hypothetical alternative networks (random site selection, EU-level optimal selection, and effectively independent prioritization in sub-units (the Member States and biogeographical regions)). This procedure allowed evaluating whether species coverage in the present N2k network more closely resembles an optimal EU joint prioritization or a more regionalized one. Instead, in Chapter IV, the SPA network was compared to a slightly different-sized network (IBAs) and therefore, an area normalization procedure was applied in order to compare the density (efficiency per area unit) of species coverage in separate networks. Statistical tests (e.g. Kruskal–Wallis one way ANOVA, Mann-Whitney *U* tests) were conducted in order to explore the differences in species coverages by these networks. All statistical and GIS analyses were conducted with ArcGIS 10.2 (ESRI, 2015), SPSS 22 (IBM Corp, 2013) and R 3.2.2 (R Core Team, 2016).

Representativeness can be interpreted in a broader sense, as the degree to which a PA network satisfies the requirements of adequacy and comprehensiveness (Margules and Pressey, 2000). In the context of Chapters III and IV, I refer by "representativeness" and "representation" to mean or median species' coverage by a network. Representation usually refers to the occurrence level of features in a specific area, and it can be measured as abundance, density, probability of occurrence, or habitat coverage (Ferrier and Wintle, 2009). In this thesis, occurrence level is measured in terms of coverage of suitable habitat (Maiorano et al. 2013). In turn, I measured efficiency as the gap between the representation achieved by optimal allocation of sites (by spatial prioritization) and the one attained by the existing N2k network.

4. RESULTS AND DISCUSSION

Here, I summarize the most important findings of this thesis and discuss how they relate to the general objectives set in the beginning of the thesis. For detailed descriptions of individual results, see the Chapters cited.

4.1 UNDERSTANDING THE CONCEPTUAL BACKGROUND OF KEY CONCEPTS AND PRINCIPLES CAN AID CONSERVATION PLANNING

SCP frequently involves a number of concepts and principles, such as complementarity and representativeness (Margules and Pressey, 2000; Possingham et al. 2006). These concepts display prominently in the SCP literature, but variable definitions and usages can be found easily, leaving uncertainty as to what the concepts actually mean. Chapter I focused on twelve common core concepts of SCP literature: adequacy, comprehensiveness, representativeness, representation, complementarity, threat, vulnerability, effectiveness, efficienc , irreplaceability, flexibilit , and replacement cost (Figure 4). Generally speaking, these selected terms are relevant for goal-setting and are associated with the process of defining conservation objectives or solutions of reserve selection problems (Lehtomäki and Moilanen, 2013). The aim was to review the historical and philosophical meanings of these concepts and examine how these concepts are interrelated and defined. The starting point for the investigation was that these concepts should be understood together, as a joint set, rather than focusing on defining them separately.

Chapter I revealed that there are multiple (also conflicting) alternative definitions for the twelve core concepts and found that not all conceptual and operational definitions were totally clear and mutually compatible. While complementarity is often called as the fundamental concept of SCP (Margules and Pressey, 2000) the traditional definition (i.e. the number of targets covered by addition of sites) is closely linked to a specific optimization method proposing sets of alternative sites (target-based planning). It would be preferable to use this fundamental concept without reference to a particular type of optimization algorithm. Therefore, the interpretation of complementarity introduced in Chapter I differs from the traditional one, providing more flexibility also regarding the computational method: generalized complementarity can be seen as how effectively conservation actions work synergistically together. Another interesting result in Chapter I was that the so-called "CAR"-concepts (comprehensiveness, adequacy, and representativeness) are widely used but they have variable and overlapping meanings. When defining CAR-concepts as a joint set this confusion is avoided: comprehensiveness and adequacy can be seen as properties of a conservation objective, but representativeness should be instead interpreted as a property of a solution (Figure 4; Chapter I). While some concepts such as representation or efficiency have relatively well-established and clear definitions in SCP, some other concepts such as effectiveness remain somewhat vague. That said, holistic concepts such as effectiveness cannot always be defined in quantitative terms in prioritization. Overall, Chapter I introduced compatible definitions for the set of core concepts in SCP (Figure 4), and thus reduced general linguistic uncertainty in the field

The present work (Chapter I) emphasizes that many of these key concepts have direct and indirect associations with older concepts and theories of spatial ecology. For example, adequacy and representativeness are closely linked to island biogeography theory, species-area relationships, and

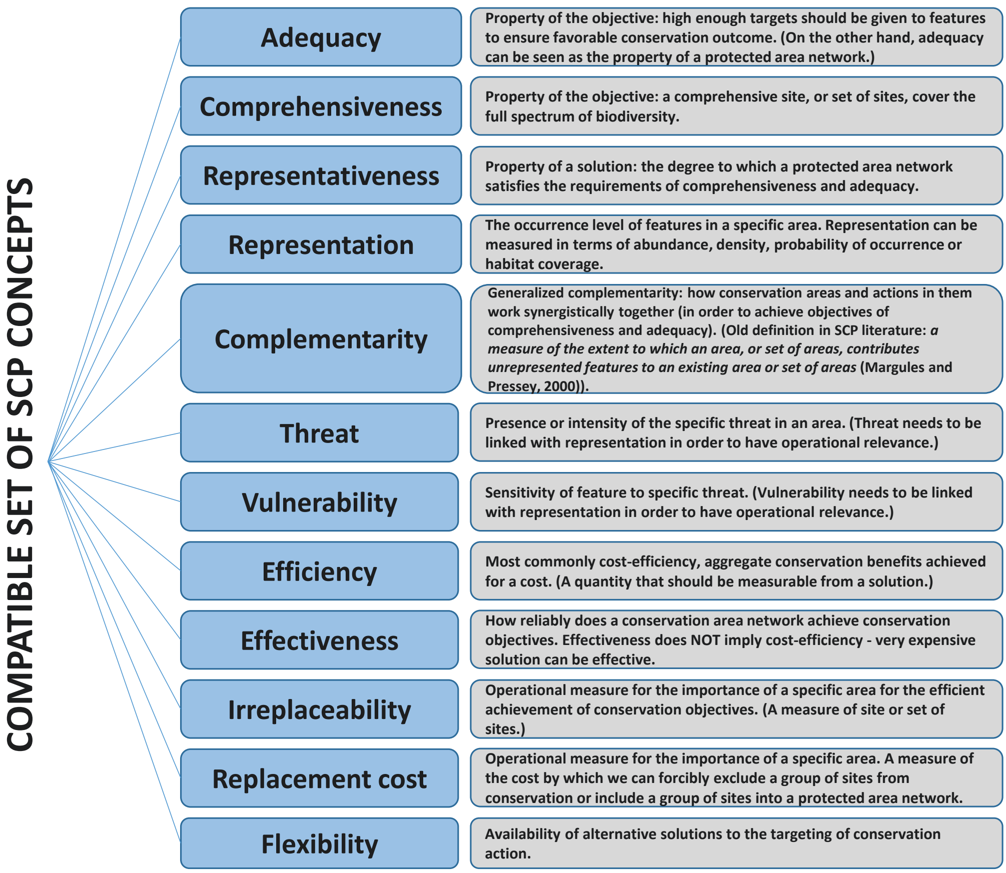


Figure 4. The twelve core concepts of SCP and definitions relevant for describing conservation objectives and operational measures or solution for reserve selection problems. Note that these concepts may have multiple alternative definitions in the SCP literature (see Chapter I for details), but the definitions introduced here are clarified so that they work well in synergy as a joint set.

metapopulation dynamics discussing about the selection criteria and optimal size for a PA network (MacArthur and Wilson, 1963; Hanski, 1998). Recognizing such heritage, this work also clarifie the history of these concepts, showing how SCP builds upon an ecological background. The SCP process includes the design of an ecologically based model of conservation value (Lehtomäki and Moilanen 2013). This stage usually involves discussion about these core concepts and principles. Good knowledge of the fundamental basis and clear definitions of SCP concepts can facilitate both prioritization and interpretation of the results. Conservation science has a multi-disciplinary scope, and with people from various backgrounds involved, it is pivotal that stakeholders understand each other (Knight et al. 2011). Overall, clarity about terms and concepts used is likely to promote successful collaborations, planning, and ultimately, better conservation outcomes.

Conclusions: While this work highlights the importance of understanding the background and origins of SCP, it demonstrates the need of clarifying and understanding the key concepts of SCP. When these concepts are defined as a mutually compatible and minimally overlapping set, they can better aid the spatial prioritization process and conservation planning. It is a vital issue how conservation scientists communicate with each other but also with varied groups of stakeholders.

Future prospects for research: New ideas and challenges in conservation science and planning may yield new needs for the development of a core set of relevant concepts. This work did not analyze concepts linking to the socio-political component of SCP or to ES. Hence, further concepts may appear useful in the future. While I highlight the importance of further discussion about terminology and concepts in SCP, future research could also focus more on the planning process itself and how conservation objectives and prioritization results are communicated and understood in practice.

4.2 ECOSYSTEM SERVICES CAN BE INTEGRATED INTO SPATIAL CONSERVATION PRIORITIZATION, BUT CONNECTIVITY REQUIREMENTS OF INDIVIDUAL ECOSYSTEM SERVICES MUST BE ACCOUNTED FOR IN PRIORITIZATION

To date, SCP methods have commonly been used for identifying spatial priorities for biodiversity. ES have been a largely untreated component in SCP, albeit present research has increasingly argued for the incorporation of ES (Cimon-Morin et al. 2013). While spatial biodiversity surrogates, such as species distribution maps, have similarities with ES surrogates, it seems that ES cannot be treated exactly in the same way in spatial prioritization (Luck et al. 2012). In this thesis, I examined the notion that SCP has potential to broaden its scope to ES. In particular, I focused on connectivity requirements of ES, as those seem to differ from the connectivity requirements of biodiversity in general.

Chapter II introduced a novel typology for connectivity requirements of ES and found that the ideal spatial priority pattern for ES may differ at least in terms of: 1) local supply area size, 2) regional network requirements for the maintenance of ES provision, 3) flow between provision and demand, and 4) the degree of dispersion that is needed for ES provision and access across different administrative regions. The results demonstrate that there are substantial differences between individual ES in terms of their connectivity requirements (Table 2). For example, carbon sequestration may have relatively low requirements for local area size and flo , but pollination requires high localized flow between provision and demand.

The work also shows how to technically integrate ES into spatial prioritization in Zonation (Figure 5). Zonation includes multiple technical solutions for accounting for connectivity, including connectivity of ES. Some of these solutions are applicable already in the data pre-processing whereas others operate during the prioritization itself or can be considered to some extent in post-processing analyses. For example, local provision connectivity (aggregation) can be taken into account by using the distribution smoothing and boundary quality penalty techniques (Moilanen et al. 2014). Chapter V introduced a novel technical solution to account for ES demand and flow: proximity between demand and supply was taken into account by entering separate pre-computed feature layers for each ES flow area. An alternative way to account for ES flow in Zonation would be to use the connectivity interaction feature which emphasizes areas where two features (provision and demand) occur nearby. Likewise, ES dispersion can be accounted for by entering different feature layers for different areas. In Chapter V, area was divided according to NUTS (a hierarchical system

Table 2. Illustrative examples of connectivity considerations for selected ES, following the most well-known classification into provisioning, regulating, and cultural ecosystem services (CICES 2016). Note that connectivity requirements (provision, flow and distributed access) can apply to an individual ES simultaneously. Table adapted from Chapter II.

ES CATEGORY	LOCAL AREA REQUIREMENTS	REGIONAL NETWORK-TYPE CONNECTIVITY	DEMAND FOR ES FLOW	NEED FOR DISTRIBUTED ACCESS
Provisioning services	Maintenance of ecosystem processes may imply minimum area size for successful ES provision; e.g. hunting, fishing. Also logistical considerations may favor larger areas: e.g., cultivated crops. e.g. ground water, whole ground water area requires maintenance	Maintenance of viable (ecological) networks needed for provisioning services that depend on biodiversity or ecosystem processes and function. e.g. anything depending on biodiversity; river systems	Logistical requirements between ES provision and beneficiaries: low to high requirements. e.g. cultivated crops (accessibility is important, although commonly transported long distances) e.g. wild food, often utilized in-situ, flow only at short distances	Considerations of security or equitable provision imply distributed supply. e.g. drinking water
Regulation and maintenance services	Large variation in local area requirements between different ES e.g. carbon sequestration, low local area requirements e.g. pollination, can be provided by smallish but high quality areas e.g. flood regulation, large enough areas required	e.g. biodiversity-dependent services including pollination: maintenance of (meta)populations needed via sufficiently dense networks of populations e.g. flood regulation, maintenance of landscape quality at catchment scale	Large variation. e.g. carbon sequestration, low local flow requirements e.g. air quality regulation, high local & regional-scale requirements e.g. pollination, high localized flow requirement	Largely same as above. e.g. air quality regulation: service desirable for all people e.g. flood regulation, service desirable for all people in flood-prone environments
Cultural services	Requirement highly variable. e.g. sense of place, no specific area requirement e.g. green areas for recreation need to be large enough	Variable requirement. e.g. sense of place: networks not needed necessarily e.g. outdoor recreation: connected network of green areas may be preferable	Requirement for flow is high: cultural services needed where there are people. e.g. recreation; accessibility of local recreational areas	High requirement for distributed supply and access. Globally aggregated supply very unsatisfactory

for dividing up the economic territory of the EU; Eurostat, 2016a) areas in the EU. Alternatively, ES dispersion can be accounted for by using the administrative units function in Zonation. (Please see Chapter II for details.)

Based on the present results (Chapter II and V) ES priority areas can be identified using spatial prioritization by Zonation and ES can be incorporated as individual data features in prioritizations (Figure 5). Obviously, ES layers can be included together with biodiversity layers, which describe distributions of e.g. species or habitats. Nevertheless, the appropriate technical solutions for a successful prioritization analysis depend on the input data and conservation objectives. As it may be difficult to assign feature-specific quantitative representation targets for ES (Remme and Schröter, 2016), Zonation provides an applicable method for prioritization because it does not require setting targets (Di Minin and Moilanen, 2012). This work raised important considerations about interactions, synergies and trade-offs between ES and biodiversity that clearly would benefit from

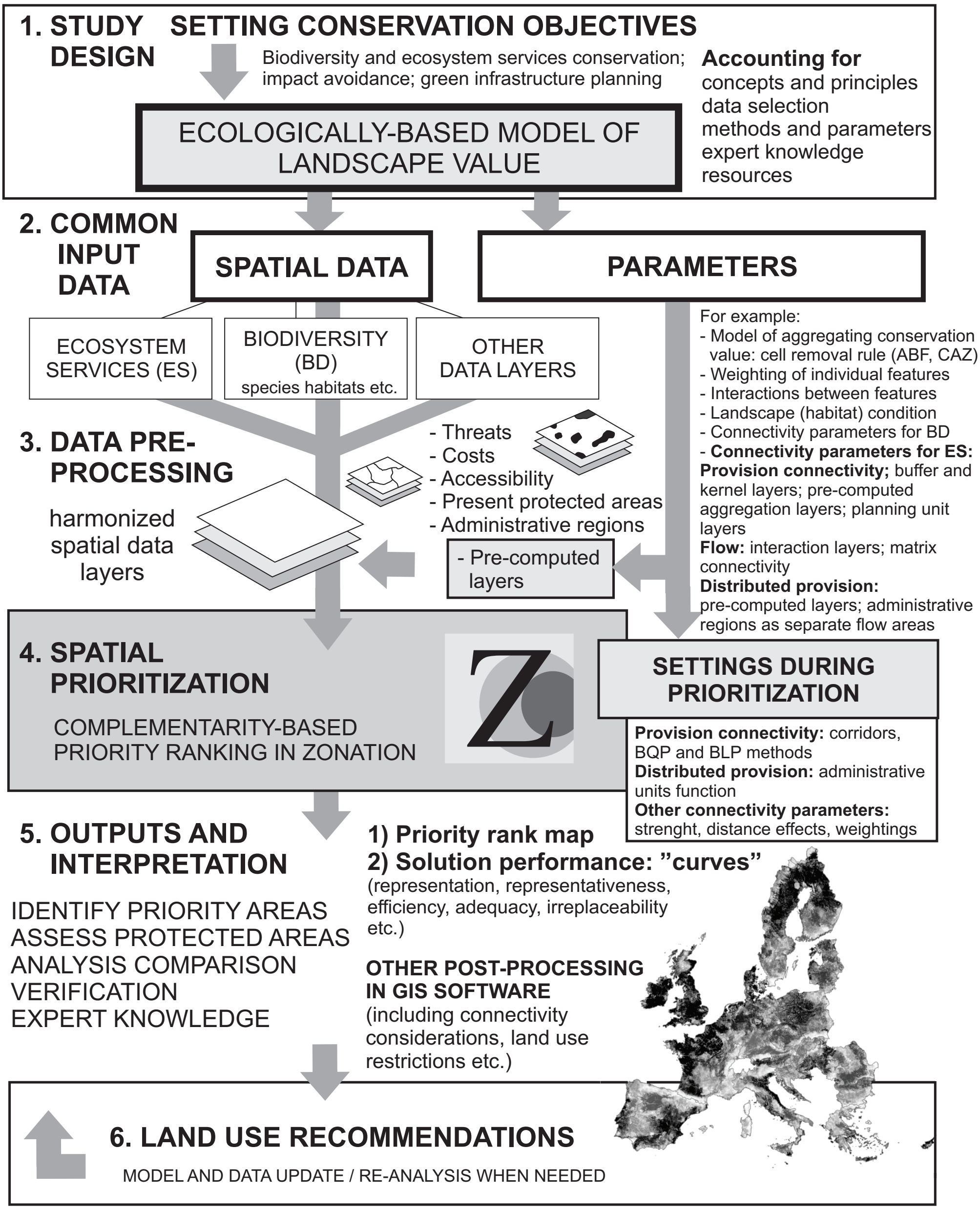


Figure 5. Schematic illustration of the process of SCP in Zonation software, involving both biodiversity and ecosystem services. Adapted from Chapter II.

further clarification technically and methodologically. As ES are a diverse set of features ranging from abiotic flows to recreation (CICES, 2016), some of them may be in conflict with maintenance of biodiversity. Zonation can take into account positive and negative interactions for example via interaction matrices (Moilanen et al. 2014). Nevertheless, it may be a challenge to integrate trade-offs into SCP, especially when the number of input features increase to thousands or tens of thousands. Inevitably, some methodological issues remain unsolved.

Finally, inclusion of ES into SCP may have far-reaching implications regarding the prioritization process, goal-setting, and the ecological model of conservation value (Figure 4; Lehtomäki and Moilanen, 2013). While some ES are valued from different socio-economic perspectives, a shift in focus is likely to occur when multiple ES are integrated into prioritization alongside biodiversity features. These considerations bring SCP closer to the socio-political component of systematic conservation planning and other land use planning (Reyers et al. 2010). Yet it is not clear what concepts and principles are most important for the ES component of SCP. Ideally, the set of concepts utilized in a conceptual model should be clear, but the ES concept itself has not yet reached such clarity. Future development in ES science and mapping will likely aid inclusion of ES into SCP as the underlying links between ecosystem functions, biodiversity, and ES become elucidated. While progress is to be expected, ES are much about human needs and valuations, which may change over time. This, as a further complication, introduces additional uncertainty into the prioritization of ES.

Conclusions: Integrating ES into SCP alongside biodiversity can provide more comprehensive and integrative results to support land use planning decisions. Successful integration of ES requires, however, special consideration on how spatial connectivity requirements of individual ES are accounted for in prioritization. While there are at least four types of connectivity influencing spatial priority patterns, individual ES have substantial differences in terms of their connectivity requirements. Spatial prioritization by Zonation serves as a useful method for identifying priorities, because Zonation enables multiple alternative technical solutions accounting for connectivity. Technical solutions should be chosen with care, paying attention to high-level conservation goals and available data. The methods introduced here can be directly useful, for example, in the development of green infrastructures.

Future prospects for research: Increasing knowledge about ES provision, demand, and spatial relationships is a worthwhile goal. There is a great need for case studies taking into account multiple ES and including their connectivity requirements in prioritization. While some individual ES may have synergistic relationships between other ES and biodiversity, there may be cases when features have negative interactions. Hence, it would be useful to investigate how to treat interactions and uncertainties related to ES provision and demand in prioritization. Finally, integration of ES into SCP would benefit from conceptual clarity and research focusing on the links between SCP and other land use planning.

4.3 THE NATURA 2000 NETWORK IN VERTEBRATE SPECIES CONSERVATION: MODERATELY SUCCESSFUL BUT ROOM FOR IMPROVEMENT

The Natura 2000 network (N2k) represents the main area-based conservation instrument in the EU, aiming at adequately securing all species and habitats listed in the two nature directives (EC 2011b). Ultimately, the high-level aim has been to create an ecologically well-performing, representative, large-scale PA network that safeguards European biodiversity (EC, 2011a). In this thesis, I focused especially on species listed in the Birds and the Habitats Directives and examined their coverage in the N2k and its sub-networks (Chapter III). Second, I compared species representation to random and optimal allocation of sites in same-sized hypothetical PA networks.

The key result in Chapter III was that the present N2k on average covers 34% of the ranges of all vertebrate directive species and performs significantly better than random allocation of sites (18%) (Figure 6). Nevertheless, the performance of N2k did not reach the level of optimal allocation of a same-sized PA network (60%). All modeled vertebrate species' distributions overlapped at least partially with N2k and its sub-networks (Chapter III, IV), indicating that there are no complete gap species in the network. Habitats and birds directive species had significantly higher coverage than non-directive species. On average, representation levels by N2k were highest for directive reptiles (36%) and directive birds (35%), whereas directive amphibians (32%) and mammals (30%) had lower representation. The largest potential for increased coverage was found for reptiles (40% increase) and for amphibians (35% increase). In addition, amphibians and reptiles had relatively small range sizes compared to mammals and birds (Chapter III). Species range coverage in the N2k generally increased with threat level (IUCN Red List status). Nevertheless, there were some (threatened) vertebrates with low representation (<10%) in the N2k, even though a higher coverage could have been achieved with the optimal allocation of sites (see Chapter III for details). Moreover, there were major differences in the extent of coverage of N2k and its sub-networks across the Member States (Chapter III, IV).

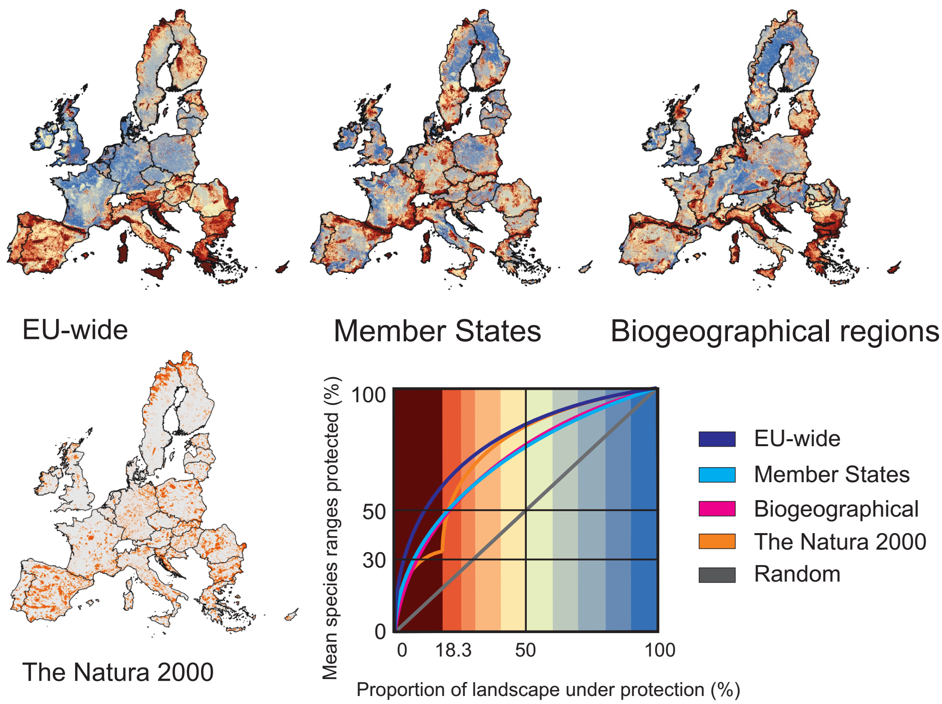


Figure 6. Spatial priorities for all vertebrate directive species presented for each hypothetical administrative planning scenario with the same color scale. Here, areas have been zoned to graded colors based on their priority rank, with highest priorities (top 18.3% of EU area) shown in red. Performance curves are presented for all five prioritization scenarios and they report the mean proportion of vertebrate directive species' ranges at different stages of the landscape ranking. For example, when 18.3% of land is under protection in the N2k scenario, on average 34% of species ranges are covered, while the EU-wide scenario can on average cover 60% of species ranges with the same 18.3% of land. (Figure modified from Chapter III).

All this information can serve as a useful source for further assessment and development of the N2k network. For example, information about PA coverage, species' range size, and representation levels in the N2k suggest which species or taxa to focus on in terms of future conservation assessments and allocation of spatially explicit management actions. For instance, it would be informative to locate from the results maps which areas outside the N2k have the highest concentrations of species with low representation and, thus, potential for increased coverage in the N2k. These areas would likely be the ones benefiting the most from future conservation effort. However, some of the species with low representation in the N2k were wide-range species or species having the majority of their distribution range outside the EU (e.g. *Pteromys volans*). Narrow-range species, such as many amphibians and reptiles, would also benefit from assessments. It may be easier to find additional small areas outside the N2k for species with small ranges than large ones.

While PAs are typically the most effective conservation mechanism for range-restricted species (Watson et al. 2014), wide-spread species may need other conservation mechanisms as it is difficul to protect them in a relatively small fraction of land. Due to the present landscape fragmentation and expected changes in future land use (Araújo et al. 2008), it clearly seems that N2k alone will not be enough for maintaining all biodiversity in the EU. The Aichi Target 11 aspires to create a global conservation system that is built not only from PAs, but also from "other effective area-based conservation measures" (Jonas et al. 2014; Juffe-Bignoli et al. 2014). Linkages between habitat patches have long been considered an important conservation strategy (Hanski, 1998; Hodgson et al. 2011). It has also been recognized previously that the Member States consider connectivity poorly in the implementation of the N2k (Opermanis et al. 2012). However, there isn't yet any operational indicator available to measure "connectivity" as described in Aichi Target 11 (Juffe-Bignoli et al. 2014). Connectivity conservation and conservation in and outside N2k should be better linked to other area-based conservation mechanisms, e.g. via green infrastructures promoting multifunctional land uses or other area-based policy instruments such as agri-environment schemes (Kleijn et al. 2006; Whittingham 2011; Liquete et al. 2015).

Conclusions and policy recommendations: The Natura 2000 network provides significantly higher coverage of species listed in the Birds and the Habitats Directives than non-directive species, implying that the present network performs relatively well in securing these target species. Nevertheless, species representation by N2k did not reach the level of optimal allocation of sites and there are still some directive species poorly represented in the network. Due to these deficiencies and substantial differences in the N2k coverage between countries, complementary conservation schemes may be needed alongside PAs in the EU. SCP methods can be effi ient in delivering policy-relevant information about species representation by PAs and overall spatial diversity patterns at large scales. This information can be further used in targeting funding and management actions to locations that effectively preserve species with inadequate representation in the N2k. EU-level decisions about the development of N2k should be carefully assessed based on ecological evidence.

4.4 COORDINATED IDENTIFICATION OF SPATIAL PRIORITIES RESULTS IN MORE EFFICIENT CONSERVATION PLANNING OUTCOMES, BUT EFFICIENCY IS ALSO MORE THAN JUST AN ECOLOGICAL MEASURE

The Habitats and Birds Directives and the EU site selection clearly implies that planning should be implemented irrespective of political boundaries (EC, 2009; Evans 2012). In this context, I examined whether the species coverage and spatial pattern of the N2k better reflect a community effort or interests of independent Member States. Spatial prioritizations were performed separately at the EU, Member States and biogeographical scales, testing hypothetical planning outcomes at different administrative levels (Chapter III).

This work showed for the firs time that EU-wide coordinated conservation planning leads to substantial efficiency gains (Chapter III). The EU-wide planning scenario, representing fully coordinated conservation planning, covered a higher mean proportion of species ranges (60%) than the present N2k (34%), Member States (47%), or the biogeographical areas scenario (46%), and this difference in efficiency repeated itself across all taxa. Furthermore, there were major differences in terms of spatial priority patterns between the scenarios (Figure 6; Chapter III). The N2k sites overlapped more with the EU-wide allocation and they were more evenly distributed across the EU compared to sites in other hypothetical optimal allocations. The third interesting observation was that the biogeographical prioritization scenario performed significantly better (median coverage 66%) for species listed in the Habitats Directive compared to the Member States scenario (median 48%) (Chapter III).

These results raise important policy-relevant questions and highlight the fact that it is crucial to understand the potential ecological efficiency loss that arises from planning that divides conservation effort into ecologically arbitrary subunits. The question about efficiency also links to ecologically arbitrary area targets. For example, the CBD Aichi target 11 has often been interpreted so that all independent countries should protect 17% of their land area. There is a risk that the target may be implemented irrespective of considerations on ecological quality and heterogeneity of the included sites. Such area-based quantitative PA targets may not be the best option for conservation planning, as they ignore ecological realities. Nevertheless, most of conservation planning is still implemented in semi-independent administrative units (Dallimer and Strange, 2015), albeit planning has incorporated “ecological units”, e.g. catchments, ecoregions, etc. (Klein et al. 2009). The EU has considered these aspects in the site selection of SCIs (the Habitats Directive) (EC, 2014b). Indeed, involving a biogeographical component in the site selection process is a way forward to more coordinated conservation planning and ecologically effective PA networks. Moreover, as the EU-wide coordinated planning scenario yielded the highest efficienc , it would also be useful to consider what is the role of the EU’s area-based conservation mechanisms in the context of broader coordinated conservation planning, e.g. as part of a Pan-European ecological network, the Emerald network (EEA, 2012). Hence, considerations about the ecological coherence of the N2k could be more effectively extended beyond the EU-28 borders, taking into account other PAs and conservation priorities in the vicinity of the EU.

The present analyses were consistent with several patterns that have been observed previously. First, vertebrate diversity is unevenly distributed and there are large-scale (latitudinal) richness gradients in the EU (Baquero and Telleria, 2001; Maiorano et al. 2013). Both Chapters III and IV showed that the locations maximizing EU-wide vertebrate species representation are highly biased towards the southern Member States (Figure 6). Second, hypothetical planning scenarios (Chapter III; Figure 6) also revealed major concentrations of priorities especially in the southern, eastern, and northern borders of Member States and the EU. These patterns are visible because species distributions and richness gradients intersect borders and "complementary" sites that differ most in their species composition tend to be located far away from each other, near border areas. This phenomenon has previously been called as an "edge artefact" (Moilanen et al. 2013; Pouzols et al. 2014), and this work confirmed it for the first time at the level of the EU.

In this thesis, I focused only on ecological measures of efficienc . In particular, I measured efficiency as the gap between species representation achieved by optimal unconstrained allocation of sites and representation attained in other more constrained prioritization scenarios (Chapter III). Observed species richness patterns and the EU-wide coordinated conservation scenario (Figure 6) suggest major additional conservation responsibility for the southern EU. However, such a theoretical EU-wide allocation of priorities may not be politically feasible. These optimal allocations, which aimed at maximizing species' representations, are optimums only in the ecological sense. Results obtained by ecologically-based spatial prioritization should, therefore, always be interpreted and balanced against local values and socio-political considerations. Nevertheless, biodiversity can only be protected where it occurs, which means that the ecological reality of priority patterns should be a fundamental consideration for decision makers.

Conclusions and policy recommendations: EU-wide coordinated planning can yield higher conservation efficiency than planning in independent administrative subunits, such as Member States. Thus, there would be additional efficiency to be gained from more effective and coordinated Member State collaboration, which could perhaps even extend outside the EU borders as well. Collaborative conservation should be emphasized when making decisions about potential network expansions and complementary area-based conservation actions. While southern Member States are core areas for EU's biodiversity, it is crucial that the EU carefully considers how conservation responsibilities and funding are shared. Rather than focusing on quantitative area targets (such as the Aichi target 11) it would be better to emphasize ecological quality and complementarity of PA networks. The biogeographical component in future site selection and assessments may further facilitate this objective. In addition to ecological measures of conservation efficienc , there is a need to consider efficiency as part of a wider socio-ecological system, regarding land use constraints and socio-economic realities in planning.

4.5 TWO NETWORKS DESIGNED FOR BIRDS BENEFIT ALSO THE CONSERVATION OF OTHER VERTEBRATE SPECIES

Surrogacy is a frequently discussed topic in conservation biology. According to its definition surrogacy is about whether we can use a specific group of species as a proxy for broader biodiversity (Margules and Sarkar, 2007; Rodrigues and Brooks, 2007). In Chapter IV, I investigated the sub-network of the N2k, the Special Protection Areas (SPAs), described in the Birds Directive (EC, 2014a) and the Important Bird and Biodiversity Areas (IBAs) defined by BirdLife International (Heath and Evans, 2000). Both of these networks were originally identified with a focus on particular bird species of conservation concern. Here, I quantified the representativeness of terrestrial SPAs and IBAs in terms of the coverage they provide to the distributions of a larger set of birds and other vertebrates (amphibians, reptiles, and mammals). Second, I investigated how IBAs have served as a source for designation of SPAs.

A key result was that on average, the present SPA network covered 23% of the suitable habitat of the birds, 31% of the reptiles, 25% of the amphibians, and 20% of the mammals. Likewise, IBAs covered 25% of the suitable habitat of the birds, and 34% of the reptiles, 28% of the amphibians, and 22% of the mammals (Chapter IV). These are impressive numbers given that the SPAs and IBAs were originally aiming at protecting mainly birds. Thus, these results raise further questions about the surrogacy potential of both SPAs and IBAs, also for other taxa than vertebrates. One interesting observation was that coverage of all vertebrates was significantly higher in locations covered only by IBAs when compared to SPAs. These areas covered by only IBAs likely include high concentrations of vertebrate species in the EU, and could potentially serve as useful information to future network assessments and expansion. It would be feasible to dig deeper into these results with SCP tools: these sites and their species composition would indeed be worth of further research.

My results also support previous global research showing IBAs to be important sites for also non-avian taxa (Brooks et al., 2001; O'Dea et al., 2006; Butchart et al., 2012, 2015). The results are also in line with previous data that IBAs significantly informed the EU-wide designation of SPAs (Stroud, 2011; Evans, 2012). In particular, the results confirmed that IBAs and SPAs overlap extensively, and they have been used especially in the site designations by the newest Member States. These findings imply that at least some of the Member States have rather extensively utilized data provided by a non-EU organization, that is, BirdLife International.

Conclusions and policy recommendations: IBAs and SPAs are two networks originally designed for bird species conservation. This work clearly shows their surrogacy effectiveness in the EU as they can contribute the conservation of other vertebrate species groups as well. Information about high-quality SPAs and IBAs could be used to support spatially explicit conservation management decisions but also to direct future assessments, for example seeking potential locations maximizing coverage of taxa other than examined here. Finally, this work also highlights the fact that IBAs have served as a significant source for SPA designation, indicating that implementation of continental-wide policies, such as the Birds Directive, can be substantially informed by data provided by NGOs.

4.6 SPATIAL CONSERVATION PRIORITIZATION CAN EFFECTIVELY INFORM PROTECTED AREA NETWORK EXPANSION OR SITE REVISIONS

While the global PA network has frequently been under assessment (Rodrigues et al. 2004a; Kullberg et al. 2015), some studies also have applied gap analysis for finding effective solutions for PA network expansions (Rodrigues et al. 2004b; Pouzols et al. 2014). I applied an expansion analysis for Special Protection Areas (SPAs) in Chapter IV using the hierarchical prioritization method in Zonation (Moilanen et al. 2014). A key observation was that identifying and adding unprotected areas into the current SPA network (increasing the extent from 12.5% to 17% of the EU) would almost double the mean coverage of bird species distributions (from 23% to 40%). Interestingly, these expansion sites were located across all Member States, apart from Luxembourg, but there were notable differences between countries. Most of the potential areas to maximize species representation for birds outside the SPAs were in southern and northern Europe (e.g. Finland, Greece, Spain). Another important observation was that 9.6% of the pixels for expanding SPA coverage to maximize bird species representation fall within existing IBAs.

This discovery raises important policy-relevant questions about the need and likelihood of future PA expansions in the EU, but also about applicable methods and practical implementation. As additions of new N2k sites have been slowing down (EEA, 2012; Evans, 2012), it is unlikely that the N2k should experience major expansion in the near future. Nevertheless, the EU has promised to be part of the implementation of the resolutions of the UN Convention on Biological Diversity, meaning that each Member State is responsible for expanding its PA network approximately to the same 17% coverage of land (CBD, 2016). Also the 15% habitat restoration target (Egoh et al. 2014; Kotiaho and Moilanen, 2015; CBD, 2016) would ideally require major area-based conservation effort. Some Member States have relatively large pre-existing national PA networks while others have PA coverage less than the required 17% (EEA, 2012; EC, 2016). As I already discussed in section 4.4, in practice, an equal percentage, such as the 17% target, may not be the most effective solution, because it does not guarantee balanced biodiversity coverage due to variation in species richness gradients across the EU. Area size has been a surrogate for adequacy in conservation biology multiple times in the past, but it is not necessarily the best measure because of landscape heterogeneity and variable area requirements of different species (Svancara et al. 2005; Margules and Sarkar, 2007). While being ecologically suboptimal, equal percentages such as the 17% target may be the political reality in the future due to policies such as the CBD. Hence, there may be demand for N2k site assessments or revisions in the future when it may be also possible to replace underperforming areas with better alternatives. If that will be the case, SCP tools such as Zonation offer a way forward in identifying the ecologically most suitable locations for additional PAs as well as for restoration (Kotiaho and Moilanen, 2015).

Conclusions and policy recommendations: My work shows that there are high-quality areas for maximizing bird and other vertebrate species coverage outside the existing SPA network. Implementing relatively small additions to the SPA network in some key countries would ensure a significant increase in the network's ability to protect an even higher percentage of species. Spatial prioritization could be used as decision support if expansions for the N2k network become timely. Future site revisions and additions to the N2k should be based on rigorous ecological evidence, accounting for each Member States' own national PA network as well as their conservation planning realities (e.g. resources, funding, and management). It would be important to make sure at the EU-level that the N2k and national PAs together construct the most comprehensive and complementary PA network.

4.7 PRIORITY AREAS FOR ECOSYSTEM SERVICES CAN BE IDENTIFIED AT THE EU-LEVEL BY SPATIAL PRIORITIZATION, BUT ACCOUNTING FOR DEMAND IS CRUCIAL FOR MAKING RESULTS POLICY-RELEVANT

The EU has shown growing interest in incorporating ES into its biodiversity policies and has initiated an extensive mapping effort (MAES) for understanding ES provision at the EU-level (EC, 2013b; Maes et al. 2012a; 2016). Chapter V introduced the first EU-wide high-resolution spatial prioritization for five ES using SCP tools. The results demonstrated that when accounting only for ES provision capacity, priority areas will likely have high ecosystem functioning but they do not adequately connect ES provision with demand by the society. This is fundamentally due to lack of connectivity between ES provision and demand (Chapter II). In other words, areas with high ES provision are more likely located in remote areas while ES demand is concentrated in areas with a high population density. The level of ES maintained by the top priority areas clearly increased after accounting for ES demand, especially for ES with small flow zones (Chapter V). Thus, it is vital to consider the proportion of the capacity that fulfills a demand rather than capacity *per se*. Previous research has also found that priority areas for ES provision capacity and demanded ES capacity do not necessarily coincide (Chan et al. 2006; Cimon-Morin et al. 2014).

Another key result in Chapter V was that when accounting for the flow zone either through administrative areas (NUTS) or ES-specific flow areas, priority areas were more evenly distributed across the EU. These observations link also to policy-relevant discussion about equality in terms of ES access (Chapter II). Thus, it may be of high interest also for policy-making in the EU how to ensure regional equality in terms of ES. In conclusion, incorporating ES into SCP should always account for ES demand to identify effective priority networks for ES. However, assessments identifying ES priority areas based on only ES provision capacity serve as useful information when assessing potential future ES demand.

Overall, there is extensive potential to expand research around ES and SCP (Luck et al. 2012; Snäll et al. 2015). Future analyses at the EU-level could consider threats to ES provision, costs of actions to protect ES (cost-efficiency), and availability of alternatives to ES provision (flexibility Chapter I). For instance, alternative land uses (Moilanen et al. 2011) or costs could be feasibly integrated into prioritization by Zonation (Moilanen et al. 2014). Due to the observed importance of ES demand and individual flow zones (Chapter V) it would be useful to further investigate how prioritizing ES at different scales affects results and their usability in decision-making and planning. Moreover, future research could focus on anticipating future key locations for ES demand and provision. Finally, it is stated in the MAES report by the European Commission that the mapping and assessment of ES in the EU should also include evaluation of the delivery of ES by PAs (EC, 2013b). In other words, the contribution of the N2k to the delivery of ES needs investigation.

Conclusions and policy recommendations: This work shows that ignoring ES demand in spatial prioritization may lead to identification of priority areas in remote regions where benefits from ES capacity to society are relatively small. Hence, identification of ES priority areas for conservation should in an appropriate manner account for ES demand and accessibility - some ES require connectivity of provision and demand, others don’t (Chapter II). This is highly relevant also due to equality in ES distribution and access. Accounting for ES demand improves the usability of spatial prioritization results as policy-support. Therefore, future policies and assessments in the EU should incorporate ES demand, consider potential actual ES use, and safeguard future options for ES provision across the Member States. Prioritization by SCP tools such as Zonation can effectively help in future spatial assessments for biodiversity and ES.

5. CONCLUDING REMARKS

5.1 SPATIAL CONSERVATION PRIORITIZATION TOGETHER WITH EXPLICIT SPATIAL DATA CAN PROVIDE INPUT FOR CONTINENT-WIDE CONSERVATION POLICIES

The contextual contribution of this thesis is that it introduced and applied quantitative spatial analysis for assessing continent-wide area-based policies within the European Union (Chapter III, IV and V). It has clearly demonstrated that large continent-wide PA systems, such as the terrestrial N2k, can be assessed using quantitative spatial prioritization methods and high-resolution spatial data. This thesis shows the importance of evaluating conservation policies in the EU and provides support for present decision-making. While the present EU-wide N2k network was found to be relatively successful in terms of vertebrate conservation (Chapter III), this thesis also identified several potential locations for the efficient expansion of the network (Chapter IV). In particular, the Zonation software has existing functionality for data-rich cost-efficient prioritization, and connectivity of both biodiversity and ES can be taken into account in multiple ways in prioritization (Chapter II). Outcomes of spatial prioritization provide useful information about PAs and patterns about biodiversity and ES (thus providing evidence for high-level conservation goals addressed in the EU biodiversity strategy).

The EU is committed to spatial conservation planning through the global Aichi target 11 (CBD, 2016) and the N2k is perceived as the cornerstone of the EU's biodiversity policy. Hence, concepts and methods presented in this thesis on how to prioritize areas, where, and for what, are timely and relevant. Ideally, similar high-resolution analyses would be used as decision support for example in the efficient allocation of geographically flexible conservation funding (Brooks et al. 2006; Lung et al. 2014). Similar spatial analyses utilizing various sources of spatial data can provide useful information for directing resources for other area-based conservation mechanisms, such as agri-environment schemes (Whittingham, 2011), or improving connectivity of existing PAs (Opermanis et al. 2012). Finally, these analyses can facilitate identification of multifunctional land uses as part of green infrastructures (Lafortezza et al. 2013; Liquete et al. 2015; Snäll et al. 2015) and reduce conflicts between biodiversity and other land uses.

Despite the fact that the EU has good spatial data resources hosted by several EU institutions and organizations (Hoffmann et al. 2013), there is still a lack of high-quality uniform data sets for species, habitats, and ES (Gaston et al. 2008; Cabeza, 2013). Consequently, the EU has initiated and implemented the spatial data directive, INSPIRE, in order to provide harmonized spatial data across the EU (EC, 2007). This thesis demonstrated that spatial data from different sources can be used in prioritization at a relatively high resolution (~1 km^2) at the continental extent. Future analyses could be conducted by even higher resolutions if needed and improved by using up-to-date spatial data especially regarding multiple other relevant ES. When it comes to other relevant factors in spatial prioritization, one could consider a wide spectrum of components in socio-ecological systems: costs, land use, management options, and local and social values (Arponen et al. 2010, McKenzie et al. 2013; Dallimer and Strange, 2015). While socio-political data can be integrated to some extent in spatial prioritization itself, an alternative way is to utilize ecologically-based prioritizations by interpreting and applying results in the light of wide-ranging socio-political considerations.

Finally, prioritizations conducted in this thesis are static assessments of biodiversity and ES, whereas in reality both are dynamic in space and time. Thus, there is the fundamental question of whether to prioritize based on known current biodiversity and ES distribution or to prepare for future change. For example, climate change might result in radical shifts in priorities in the future (Araújo et al. 2011; Alagador et al. 2014). That said, uncertainties, input data, and computational limitations have a direct effect on spatial prioritization (Lehtomäki and Moilanen, 2013) and therefore it is crucial to be aware of these limitations especially when interpreting and communicating prioritization results. In addition, one should consider the data quality and proper validation always when using any kind of surrogates in conservation planning. Due to these uncertainties, continent-wide spatial prioritization outcomes may be inadequate for guiding direct conservation management at the very local scale. Nevertheless, they can serve as a useful source for providing evidence about regional-scale patterns of biodiversity and ES across the continent.

5.2 SUSTAINABLE LAND USE PLANNING NEEDS INTEGRATIVE APPROACHES AND LINKS TO POLICY

The conceptual focus of this thesis has been on concepts and methodologies of the framework of spatial conservation prioritization (SCP), originally developed for identifying spatial priorities for biodiversity conservation. While SCP fundamentally derives its background from broader ecological theory (Chapter I), this thesis suggests that both the SCP framework and software are applicable to spatial prioritization of ES. This work introduced methods in the Zonation software by which it is possible to account for ES and their connectivity needs in spatial prioritization (Chapter II, V). Nevertheless, integration of ES into SCP would benefit from further examination both conceptually and methodologically. A well-established and systemic planning framework, such as SCP, has a great potential for incorporating ES, but it is crucial that key concepts and methodologies are both operationally feasible and clear enough for successful communication with multiple stakeholders. At least to some extent, SCP may help in identifying synergies between biodiversity and ES, and therefore help to recognize potential "win-win" solutions. Nonetheless, there is the overarching question about relationship between ES and biodiversity (Chan et al. 2006; Mace et al. 2012) and whether they should be included in SCP jointly or independently from each other. Rather than strengthening the juxtaposition of biodiversity and ES, it would be more beneficial to develop a unified SCP strategy that would result in greater sustainability in both areas (Schröter et al. 2014b).

Overall, SCP is a solution-oriented multidisciplinary fi ld (Reyers et al. 2010) and extremely prone to complexity, uncertainty, and incomplete data that often characterize so-called "wicked problems" in broader planning contexts (Burgman et al. 2005; Hartmann 2012). Any kind of spatial planning inevitably faces different expectations and norms, which makes on-the-ground planning inherently complex. The existing gaps between scientific knowledge, policy-making, and implementation (Knight et al. 2008; Reyers et al. 2010) extend beyond SCP into many other applied sciences, such as ecosystem services science. The plurality of definitions in terms of ES (Saarikoski et al. 2015) may be a challenge, but otherwise multiple ES approaches can be seen as enhancing multidisciplinary collaboration (Cimon-Morin et al. 2013).

It seems clear that successful biodiversity conservation outcomes cannot be achieved without multidisciplinary expertise and widespread engagement of the society as a whole. Hence, the essential question in this context is whether systematic conservation planning including SCP remains as a distinct planning paradigm or whether it moves on towards unification with other forms of spatial planning. Generally speaking, spatial planning includes a multitude of other than ecologically-based aspects (Taylor, 1998). Thus, it is worth noting that SCP and spatial prioritization in particular represent only one approach to conservation planning. For example, strategic conservation planning approaches and systematic conservation planning have been relatively isolated so far (Groves and Game, 2016). In conclusion, it is likely that SCP would benefit from complementary and integrative components. ES provide a great framework for linking SCP into socio-economic aspects of human well-being, for example through green infrastructure planning (Lafortezza et al. 2013; Liquete et al. 2015). Indeed, in order to develop a more integrative and sustainable framework, SCP effectively requires well-functioning links to general land use planning but also to policies (Pierce et al. 2005; Game et al. 2015).

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