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Highlights

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Socio-political boundaries are an inevitable part of a human-dominated world

Ignoring them imposes costs on biodiversity and ecosystem management

To address this, we suggest four research pathways which would include:

Scale-matching, mutual societal values and economic benefits, stakeholder behaviour

Why socio-political borders and boundaries matter in conservation

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Acting to demarcate the spatial limits of decision-making processes, socio-political boundaries are an inevitable part of a human-dominated world. Rarely coincident with ecological boundaries and thus having no ecological functional role by themselves, nevertheless they impose substantial costs on biodiversity and ecosystem conservation by fragmenting ownership, governance and management. Where boundaries are in place, a lack of coordination on either side of a boundary affects the efficiency and efficacy of ecosystem management. We suggest four research pathways which will enhance our ability to address the adverse effects of socio-political borders on conservation: (i) scale-matching; (ii) quantification of the mutual economic benefits of conservation across boundaries; (iii) determining transboundary societal values; and (iv) acknowledging the importance of stakeholder behaviour and incentives).

Management by boundaries

With most ecosystems appropriated for human use [1] the opportunity for large scale conservation of wilderness is lost for much of the planet. In many parts of the world, ecosystem management and biodiversity conservation must occur largely in the context of human-dominated landscapes. These landscapes can be heavily fragmented in terms of habitats [2,3] and are criss-crossed by socio-political boundaries which determine ownership, governance and management. Such boundaries can have substantial adverse effects on conservation as a lack of coordinated actions by those on either side of a boundary impacts on the efficiency and efficacy of ecosystem management. For those interested in managing biodiversity and ecosystem services, borders and boundaries are central in helping researchers and practitioners determine probable outcomes of their interventions.

Ecological and socio-political boundaries

Landscapes can have many types of border or boundary, but two that have received much research interest are those that occur between habitats and/or ecosystems ('ecological boundaries') and those that demarcate socio-political entities, such as land tenure, municipalities, planning jurisdictions, protected areas, regions and nation-states ('socio-political boundaries').

Boundary concepts are some of the most prevalent in ecology [2] and have been termed edges, ecotones, boundary layers, gradients, clines, transition zones and interfaces. The concept of an ecological boundary encompasses all these terms, and refers to '...areas of transition, contact or separation between contrasting elements of a mosaic, which are functionally connected by fluxes of organisms, material, energy and information...'[3]. Therefore, boundaries are components of spatially heterogeneous areas, and are prevalent in landscapes subject to habitat fragmentation. The importance of ecological boundaries lies in their role as structural and functional components of the

51 habitat mosaic. They therefore have direct implications for community structure and ecosystem

function in complex landscapes.

Socio-political boundaries pervade many aspects of society at multiple spatial scales from local (neighbouring landowners occupying small plots in urban settings) to global (nation-states) [4]. They are socially constructed and intended to reduce ambiguity regarding the ownership of space and how order is maintained [5]. Boundaries are, therefore, part of the practices and processes by which societies determine their territorial limits. Traditionally, boundaries have been conceived of as lines separating sovereign territories (Figure 1A), and classic political geography has defined boundaries as physical barriers that are demarked by legal, institutional and social processes. It is these borders that tend to delineate the limits of decision-making processes, however, 'territories' and 'identities' can be social, political, economic or cultural (Figure 1B). Regardless of how described, boundaries are created by the ability of populations to impose lines of separation. Geopolitical entities (municipalities, provinces, regions, and nation-states) are, therefore, central when it comes to decision-making around how boundaries and borders are implemented [6].

How socio-political boundaries can adversely affect ecosystem management

A socio-political boundary serves no ecological function because socio-political and ecological boundaries rarely coincide (Figure 1A;1C). Land parcels separated by socio-political boundaries will, therefore, commonly share ecosystems and biodiversity. Nevertheless, a socio-political boundary can affect the management of biodiversity and ecosystems, mediated through how ecosystems, and the species they contain, are subject to different governance structures, political priorities and societal attitudes on either side of the boundary.

The division of a landscape into administrative, ownership or management categories is likely to facilitate habitat change and therefore the fragmentation of contiguous land covers. The administrative zoning of land parcels into, for example, urban as opposed to non-urban areas, can drive land-use change as private land-owners seek to derive income from the permitted land-uses. In the UK, policies aimed at protecting a 'green belt' of non-built-up land adjacent to major cities has resulted in a constrained supply of land for development and contributed to high property prices, thus increasing the opportunity cost for leaving land in less intensive uses (e.g., [7]). Although most private land is managed for reasons, such as farming, other than biodiversity conservation, the actions and decisions of private individuals are central to the persistence of many species. Even within the same habitat type, owners are likely to manage the land that they own differently to maximise their own welfare, which could lead to habitat changes and thus biodiversity and ecosystem service alterations. For example, in northern England, the number of species of bird found on upland farms varies according to the characteristics of the farm itself, such as land tenure and labour inputs. Farm management decisions, such as mixed grazing regimes, fertiliser input and the legal control of predators were also important predictors of avian diversity [8].

Both provincial and international borders can impose additional costs on ecosystem management [9,10]. Species ranges will regularly span multiple countries or regions, making an approach based on administrative units unsuitable for the assessment of extinction risk, or the optimal allocation of scarce conservation funds. International and within-country provincial borders have reduced the efficiency and coherence of the European Union (EU)'s Natura 2000 network of protected areas [11]. These empirical data chime with conservation management models, which indicate that gains efficacy and efficiency from coordination of conservation efforts across provincial and international borders can be significant [9,10]. For example Kark et al. [9] analysed the efficiency gains of

coordinating the conservation efforts of 20 countries in the Mediterranean basin. A fully coordinated conservation plan would save ~US\$67 billion, or 45% of the cost of the uncoordinated plan. A lack of coordination in resource use could not only result in additional costs, but also increases the likelihood of disputes between parties on either side of a border. For example, within river catchments freshwater scarcity, pollution events and infrastructure development have all resulted in cross-border disagreements [12](Box 1).

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Reducing the adverse impact of socio-political boundaries: current approaches

One way to lessen or remove the effect of boundaries is to ensure that compatible ecosystem and biodiversity management policies and practices are undertaken on both sides of a division. Indeed, securing the engagement of large numbers of private landowners is one way that larger, more cohesive, tracts of land can be managed for conservation. Economic incentives, often underpinned by multi-billion dollar budgets (e.g. agri-environment schemes in the EU), are used to encourage landowners to manage their land to increase the production of non-market environmental goods, such as biodiversity [13]. A major problem of incentive schemes is that they operate at the level of individual properties [8,14] and, therefore, rarely coincide with the spatial scale of the conservation issue that they are intended to address [15]. For example, in the Peak District of northern England, many breeding birds move across boundaries between adjoining properties during their daily foraging activities [16]. Unless all property owners are signed up to compatible management options within an incentive scheme, conservation actions are likely to be less efficient than they could otherwise be. One way to facilitate coordination between landowners is to design schemes that incentivise spatially coordinated land management. The agglomeration bonus is one possibility whereby payments that landowners receive depend on their own actions and those of their neighbours. Even though there are additional transaction costs, theory predicts that the

agglomeration bonus is an efficient mechanism for motivating coordinated actions [17]. Although some countries in the EU do encourage farmers to act jointly to achieve landscape-scale targets [14], there remain few international examples currently in operation; two such schemes are CREP (Conservation Reserve Enhancement Program) in the US state of Oregon, and 'network bonuses' paid in Switzerland [18].

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At a larger scale, ecosystems, their functions and services inevitably cross borders between provinces and internationally. Transboundary protected areas represent a well-known solution that neighbouring nation-states have used to manage ecosystems that span their borders with 112 countries coordinating the management of 818 protected areas between them [19]. Some of the better known examples are in southern Africa, such as the Kgalagadi Transfrontier Park in South Africa and Botswana. Transboundary agreements covering the supply of freshwater, such as river commissions or water collaboration treaties, are similarly common. Globally, around 280 major rivers cross international borders (TFDD 2014; www.transboundarywaters.orst.edu) and transboundary agreements are in place for ~70% of shared catchments [20](Box 1). For example, the Columbia River in North America is shared by Canada and the US. In 1964 a treaty was implemented which involved the construction of dams upstream in Canada, which the US helped pay for. The dams were intended to reduce downstream flood risk and to increase power generation. The results have been positive; Canada receives a share of the hydropower and there has been no large-scale flooding. The treaty has therefore been a success as management in one nation-state has delivered an ecosystem service (flood prevention) in another, which pays for the delivery of that service.

Transboundary protected areas and catchment management arrangements overcome boundaries by applying coordinated management on both sides, often with few parties involved. Where ecosystem and biodiversity conservation issues span a greater number of parties, some of whom might not share a physical border, treaties focussed on environmental issues might need to be implemented; a process that can be extremely complex. Nevertheless, by the late 20th century, countries were negotiating an average of 80 multi- and bilateral environmental agreements, protocols, and amendments annually (IEA 2013 http://iea.uoregon.edu) (Box 2), with some evidence that there is a synergy between trade openness, political ties and multilateral environmental cooperation [21,22].

Emerging and novel research directions

Thus far we have argued that a major challenge in addressing environmental problems is that ecosystems are dissected by socio-political boundaries. As we have seen, some solutions are already in place. However, there are many emerging and novel techniques which warrant further investigation and application. Here we outline four pathways where we think future research and practice should concentrate.

(i) The scale of management should match the scale of the conservation issue

In 2005 the Millennium Ecosystem Assessment [23] concluded that the sustainable management of ecosystems would require the global community to develop institutions at multiple scales. Although governance instruments are available at a range of spatial scales, regulatory tools and institutions rarely operate at the same scales as the ecosystems they are in place to manage [24]. Scale matching remains one of the key mechanisms through which the effects of boundaries and borders can be addressed; by aligning socio-political and ecological borders the adverse effects of socio-political borders can be removed from the system. For instance, matching the scale of management to

biogeographical regions allows biogeographical knowledge to place local assessments of species threat status within a broader context. For example, across the Carpathian Mountains in central Europe species that are in high threat categories within nation-states face reduced threats at the biogeographical level. Similarly, within Italy and Spain, plant species whose distributions straddle provincial borders are often placed in different threat categories in each province. In both cases, assigning common threat statuses could ensure resources are focussed most effectively [25]. We therefore need to match the level of governance to the scale of the environmental dilemma [26,27]. Systematic approaches have been suggested which test the fit between the spatial and temporal scales of human behaviour and the scale at which ecological resources are interconnected, although there are few applications thus far (see [28]). Social network analysis could be one promising direction to understand where mismatches might occur [29] and therefore increase the likelihood of successful on-the-ground conservation outcomes [30].

In circumstances where governance is fractured by socio-political borders, highly mobile and migratory species present a special challenge as they are likely to encounter, and cross, socio-political borders frequently and are thus exposed to many different threats and socio-political circumstances [31-33]. Therefore, there is potential for spatial and scale mismatches between the habitats that support species and governance arrangements that are in place to protect them (cf. [34,35]). Conservation actions restricted to only a subset of the required resources are unlikely to deliver substantial benefits (Figure 2). In some cases, coordination might only be needed between adjacent habitats or properties (e.g., [16]), but in many other situations successful conservation will depend on international collaboration. For example, large carnivores, such as wolves and brown bears, are expanding their ranges throughout Europe. As carnivores move across socio-political borders they are exposed to different political priorities and social norms, and their status under

conservation legislation can change radically [36,37]. Despite protests from its country of origin, a brown bear from the expanding Italian population was shot when it appeared in neighbouring Austria [38]. Wolves are now being sighted in densely populated countries like the Netherlands and Denmark, from which they have been absent for hundreds of years and where social acceptance of carnivores is low. Successful management of highly mobile species will require that individual states understand the factors influencing attitudes towards these species, harmonise their laws and develop shared ways of dealing with behaviour, such as killing domestic livestock, which some societies find less acceptable than others [38].

This need for large-scale collaboration could be one reason why many migratory species, alongside the phenomenon of migration itself, are endangered [39], not least because protecting the entire range of a migratory species is unlikely to be feasible [40]. One option would be to employ the mobile place-based approaches which have been suggested for wide-ranging pelagic species in marine conservation [41]. Although this might be more difficult in terrestrial landscapes which are split between a large number of land managers who would need to cooperate, similar instruments could be considered for the protection of all migratory species. Example mechanisms include protected areas that 'move' with the annual life-cycle of a species, or which are in place only for particular life-history stages, such as has been suggested for saiga antelope (Saiga tatarica) in central Asia [42]. As has been reviewed elsewhere [32], and attempted for shorebirds migrating between East Asian and Australasia [33], conservation planning also needs to adopt new approaches to migratory and mobile species which incorporates their dependence on multiple habitat resources across many different socio-political jurisdictions, even when those dependencies are uncertain or unknown.

218 (ii) The importance of biodiversity and ecosystem services for the material well-being of people
219 living either side of socio-political borders must be demonstrated
220 Cooperation between parties is necessarily driven by the interests of each individual [43,44](Box 1).
221 Therefore, transboundary cooperation on biodiversity and ecosystem services would be more likely
222 if economic performance and human well-being are enhanced for all parties separated by borders if
223 coordinated management takes place [23]. Ecosystem services offer one potential approach as they
224 already meet many of the criteria necessary for underpinning a potentially successful policy, not

least because their management is phrased in terms of mutual interest for diverse stakeholders

[23,34].

We have already described one application of the ecosystem service approach in relation to sociopolitical borders in freshwater supply [20,45](Box 1). Another might include the management of
vector borne diseases. Here, higher biodiversity tends to reduce transmission rates and disease
spread [46]. Thus, reaching transboundary agreements to conserve biodiversity could be
economically rational, even if they are costly to one particular party, because the benefits (reduced
risk and severity of vector borne disease outbreak) could outweigh costs. Equally, given that
migratory species transfer energy from south to north every year, transboundary agreements of all
nations within which a migratory species is found could help conserve the species and retain the
functional role of the species in south-north nutrient and energy transfer [47]. A similar argument
could be made for the cultural services that might be associated with emblematic migratory species,
such as the monarch butterfly (*Danaus plexippus*) in North America [34]. Here, citizens on both
sides of the US-Mexico border value the species, perhaps facilitating the development of
complementary management approaches throughout the species range. One possible mechanism for
the above examples (freshwater supply, disease management, migratory species) is the

quantification and establishment of transboundary "spatial subsidies" as payments for services and/or benefits used in one location but requiring other locations for maintenance and support [35].

(iii) Include the distribution of benefits from conservation actions to encourage transboundary cooperation

Biophysical and, increasingly, economic (e.g., [48]) values are used to define high priority areas for conservation. Incorporating social values in decision making is also important but to date, one missing element has been the distribution of welfare benefits that society gains from conservation actions. This is especially pertinent for many cultural ecosystem services, such as wild species diversity and landscape aesthetics, which are not pure public goods. In these cases although societal benefits decline with the distance from the ecosystem to be conserved (e.g., [49]), the general public report high willingness-to-pay to conserve species and landscapes at some distance from their home country [50]. Future work needs to include not only conservation efficiency and/or success, but also welfare gains and how they vary across, and in response to, socio-political boundaries.

(iv) Understand behaviour and incentives

Ignoring how the presence of boundaries affects behaviour and resource use can undermine the effectiveness of conservation policies. Individual preferences and behaviours affect threats to biodiversity and ecosystems as well as opportunities for restoration. For example, in the Serengeti, the distance of a village from the boundary of a protected area affects the rate of illegal harvesting within that protected area [51]. Stated preference studies have shown that the effectiveness of protected area boundaries might increase if hunters or fuelwood collectors are offered income substitutes [52]. Regulation and enforcement schemes should be explicitly designed to integrate such spatial dynamics. Similarly, where conservation depends on private landowners voluntary

participation in in conservation schemes (e.g., agri-environment schemes in the EU) there is often a problem that too few individuals take part or that resources get spent on areas of low conservation interest [14]. Researchers and policy designers therefore need to understand the drivers and barriers to landowner participation in, and commitment to, conservation. One way forward would be to include the mapping of individual preferences, their social networks and how these explicitly link with conservation opportunities in any planning and policy design process.

Future directions and concluding remarks

Socio-political boundaries can impose substantial additional costs on the efficient and effective management of the natural world. Conservation will therefore require an integrated transboundary approach to planning and management where the scales of management and ecosystems are matched. Inevitably cooperation across socio-political boundaries at multiple spatial scales will be essential, but this is only likely if researchers and practitioners can demonstrate that there are mutual benefits for human welfare for all interested parties.

Here we have focussed solely on physical, mappable boundaries, but others can be conceived, such as those that exist between disciplines or sectors. These will impose their own costs on efficient environmental management. Thus, even in cases where the spatial scale at which governance operates is the same as the ecological scale, non-cooperative behaviour between different sectors (e.g., agriculture and biodiversity conservation; NGOs from the development and conservation sectors) can be counter-productive. Therefore, there is an additional need to address cross-sectoral cooperation [45]. The research community and international organisations, perhaps through initiatives such as the recently initiated Intergovernmental Platform on Biodiversity and Ecosystem

Services (IPBES)[53], should focus conservation research on the barriers and opportunities for cooperation across the full spectrum of socio-political boundaries. Acknowledgements M.D. was supported by an EU-FP7 Marie Curie Fellowship (no. 273547). The authors would like to thank the Danish National Research Foundation for their financial support of the Center of Macroecology, Evolution and Climate. We thank Edward Game for useful comments on an earlier version of the paper.

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Box 1

Water is perhaps the most essential of all natural resources, both for economic development and ecosystem service provision. Given that rivers and their catchments are commonly dissected by socio-political boundaries, issues related to rivers and water represent one set of examples where socio-political and ecological boundaries do not match. This has led to conflict and provided pressure on states to cooperate.

The Nile and its tributaries are shared by 11 countries and more than 300 million people live by, or depend on, the river, a figure that is expected to rise to 500 million by 2030. The Nile catchment area is an example of a mis-match between borders which affects water supply, pollution and freshwater biodiversity. For instance, water extraction and human pressure in the form of pollution has resulted in increased threats to both biodiversity and water security [54]. These threats increase in their intensity further downstream as, for example, pollutants accumulate from upstream activities, which could well have taken place across an international border (Figure I).

There is a long history of disagreement regarding how freshwater from The Nile should be equitably distributed, which various treaties over the course of more than a century have tried to ameliorate. One issue is that even where treaties are in place upstream nations have less interest in complying as their benefits from the arrangements tend to be much lower than those that accrue downstream. For example, Ethiopia claims never to have ratified the 1902 Nile Treaty which prohibits Ethiopia from carrying out any activities that could constrain water use downstream in Egypt.

A more recent attempt to facilitate cooperation was the establishment of the Nile Basin Initiative (NBI) in 1999. Its main objective was to establish a framework agreement that is inclusive of all the Nile riparian nation-states. The NBI establishes the principle that each Nile Basin state has the right to use, within its territory, the waters of the Nile River Basin, and lays down a number of factors for determining equitable and reasonable use. However, Egypt and Sudan did not ratify the NBI and insisted on their original user rights. In 2011 another dispute occurred when Ethiopia initiated plans to build the Grand Ethiopian Renaissance Dam. Currently this dispute is unresolved.

Box 2

International treaties on biodiversity protection are present at three levels: global, regional, and multi-lateral. Global examples include Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES; 1973), the Convention on Biological Diversity (CBD; 1993), and perhaps of greater relevance to transboundary conservation the Convention on Wetlands, (the Ramsar Convention; 1971). It is notoriously difficult to assess the effectiveness of global-level environmental treaties [55]. Nonetheless, the Ramsar Convention includes 14 transboundary wetlands with a shared and harmonised management system (e.g., the Saloum-Niumi Complex which is bisected by the international border between Gambia and Senegal).

Regional examples comprise two-thirds of all international treaties [56], and include the Natura 2000 network of protected areas in the EU. Although there is no obligation for member states to address transboundary issues, conservation efforts across Europe are at least coordinated to a certain extent. The stability of the EU, availability of funding and the precedent of collaborative relationships across borders on non-environmental issues has enabled some transbouldary

agreements to be reached, such as the Alpine Network of Protected Areas and the Living Space Network [57] in central Europe.

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Multi-lateral agreements have been established to manage particular groups of species, such as the Convention on the Conservation of Migratory Species of Wild Animals (CMS), which was adopted in Bonn in 1979 and came into force in 1985. Contracting parties collaborate to conserve migratory species and their habitats in two different ways by: (i) providing strict protection for endangered migratory species; and (ii) reaching multilateral agreements for the conservation and management of migratory species which would benefit from international cooperation. One example of the latter is the Agreement on the Conservation of African-Eurasian Migratory Waterbirds (AEWA), which is dedicated to the management of waterbirds throughout Africa, Europe, the Middle East, Greenland and the Canadian Arctic islands. Over 250 species are managed under this agreement, including the eastern population of the pink-footed goose (Anser brachvrhvnchus). This species breeds in Svalbard, has stop-over sites in Norway and winters in Denmark, the Netherlands and Belgium. Each of these countries has different management priorities for the species; the birds are fully protected in the Netherlands and Belgium, have a hunting season in Denmark and are under an adaptive harvesting scheme in Svalbard. Despite these differences, the AEWA provides a framework through which the species can be managed and helps to ensure that the potential for over-harvesting through cumulative impacts on the geese across multiple countries is avoided. Indeed, like many geese species in north-west Europe, the pink footed goose has increased markedly in numbers in recent decades [31,58].

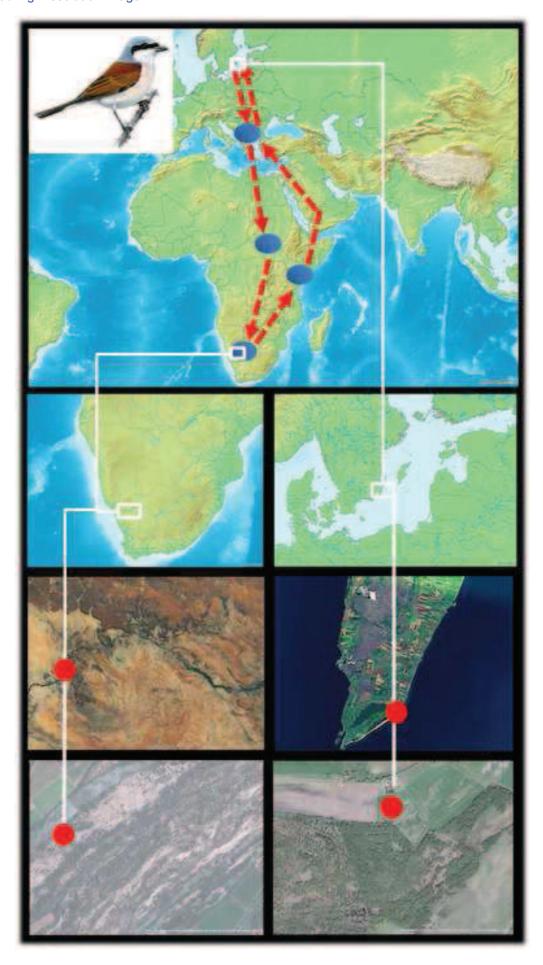
493 Figure legends 494 495 Figure 1. The geopolitical boundaries in Africa (A) are different from ethnic boundaries (B) 496 497 (www.worldmap.harvard.edu/africamap). Neither coincide with ecological boundaries between 498 ecosystems [59] **(C)**. 499 500 Figure 2. Migratory routes and staging areas for the red-backed shrike *Lanius collurio* (photo credit 501 RSPB images) [60] cross many different boundaries and multiple scales. Through its annual cycle 502 the species is therefore vulnerable to habitat changes at numerous sites. Successful conservation 503 management for this species, and many other north-south migrants, requires transboundary 504 cooperation across continents, countries, landscapes, and land parcels (cf. [32]). 505 506 Figure I. The Nile (the river catchment here indicated by the orange line) passes through 11 507 countries including Uganda, Ethiopia, South Sudan, Sudan and Egypt (A) (International Water 508 Management Institute. Research Programme on Water, Land and Ecosystems, www.wle.cgiar.org). 509 Water extraction and pollution represents a threat to both biodiversity and water security (B) [54].

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