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Supplementary material for this article is available online

Abstract

Connectivity conservation is an emergent approach to counteracting landscape fragmentation and enhancing resilience to climate change at local, national, and global scales. While policy that promotes connectivity is advancing, there has been no systematic, evidence-based study that assesses whether connectivity conservation plans (CCPs) resulted in conservation outcomes, and identifies specific plan attributes that may favor successful implementation. To fill this gap, we gathered 263 terrestrial CCPs from around the world, characterized attributes of 109 plans by surveying plan authors, and conducted semi-structured interviews with authors and implementers of 77 CCPs. The production of CCPs started around 1990 and has increased markedly in all parts of the world, most notably in the United States (led by NGOs and a few states, with little federal involvement), Europe (led by the EU and national policies and implemented at local levels), and the Republic of South Africa (where national legislation mandates each municipality to map corridors and zone all land by 2020). All of the 109 plans that we examined in detail were followed by implementation actions such as crossing structures, ecological restoration, land purchases or easements, recognition of corridors through zoning or government designation, and public engagement. Interviewees emphasized the importance of initial buy-in from key government stakeholders, stakeholder involvement beyond initial buy-in, minimizing staff turnover, and transparent and repeatable procedures. Our quantitative and qualitative analyses similarly suggested that implementation of a CCP was enhanced by enduring partnerships among stakeholders, continuity of leadership, specific recommendations in the CCP using tools appropriately selected from a large toolbox, the existence of enabling legislation and policy, a transparent and repeatable scientific approach, adequate funding, and public outreach.

1. Introduction

Roughly one million species are threatened with extinction in the face of unprecedented and accelerating rates of environmental change (IPBES 2019). Across the globe, habitat fragmentation is a primary threat to biodiversity (Butchart *et al* 2010). Fragmentation has transformed more than 50% of the planet's landscapes through the impacts of agriculture, urbanization, grazing, industrial activity, and linear barriers such as roads, railways, pipelines, fences, and canals (Jongman 2002, Gutman 2007, Jones *et al* 2007, Watson *et al* 2016). Protected areas are the cornerstone of conservation but less than 15% of the terrestrial realm has such coverage and over half of the world's protected areas are smaller than 100 ha (UNEP-WCMC 2019). Conservation science has highlighted the need for more connectivity conservation for over a half century with ever more increasing awareness of species' movement ecology and their need to shift their geographic ranges in response to climate change (Heller and Zavaleta 2009, Tucker *et al* 2018, Tabor *et al* 2019). Yet less than a third of the world's protected areas are adequately connected (Saura *et al* 2017).

Maintaining or restoring connectivity between fragmented habitats or landscape patches is the primary strategy to prevent or reverse fragmentation (Bennett 1998, Haddad *et al* 2015). Connectivity is the degree to which landscapes and seascapes allow species to move freely and ecological processes to function unimpeded (Taylor *et al* 1993). Scientific evidence overwhelmingly demonstrates that habitat connectivity promotes species conservation and ecological functions (Hilty *et al* 2019).

The importance of ecological connectivity has been recognized at global, international, and national levels. The Convention on Biological Diversity (CBD) includes ecological connectivity within Aichi Targets 5, 7, and 11. Aichi Target 11 specifically calls for 'well-connected systems of protected areas … integrated into wider landscapes and seascapes.' Connectivity conservation is gaining more traction in the upcoming ten-year strategic plans of the CBD and the Convention on Migratory Species (also referred to as the post-2020 global biodiversity framework). The European Union has different legislations such as the EU Habitat Directive as well as national-level legislation that address connectivity conservation. At a national level, Kenya and Tanzania recently joined several European countries, Costa Rica, and Bhutan as nations with national connectivity legislation. Australia and the United States (US) have pending national corridor legislation. Canada has created a Connectivity Working Group as part of its Target 1 national conservation plan, and four US states (California, New Hampshire, New Mexico, and Oregon) have enacted wildlife corridor acts; another 12 US states have wildlife corridor bills pending or just passed them in their current legislative cycles.

Many scientific papers have addressed the theory and practice of counteracting fragmentation by connecting habitat through corridors, stepping stones, or a permeable matrix (Von Haaren and Reich 2006, Rudnick *et al* 2012, Cushman *et al* 2013). This science has been used in many Connectivity Conservation Plans (hereafter referred to as CCPs or plans) such as the Yellowstone to Yukon Conservation Initiative and the Staying Connected Initiative in the US and Canada, the Albertine Rift Initiative in Africa, the Northern Tanzanian Rangeland Initiative, SOS Mata Atlántica in Brazil, the Alpine Ecological Network and the Carpathian Protected Areas Network in Europe, and the Gondwana Link and the Great Eastern Ranges Initiative of Australia. As some of the initial members of the Connectivity Conservation Specialist Group of the World Commission on Protected Areas of the IUCN that was formed in 2016, we could not find any systematic attempt to assess whether CCPs resulted in conservation actions or what plan attributes might be associated with conservation interventions (but see Keeley *et al* 2018b).

To conduct such an assessment, we gathered CCPs for terrestrial planning areas around the world. We characterize attributes of each plan, analyze traits associated with implementation, and summarize key themes that emerged in interviews with CCP authors. We provide insights into which CCP traits and practices promoted conservation implementation, and identify key factors that make for a successful CCP. We hope this review will help improve the implementation of CCPs and make science more relevant to on-the-ground conservation.

2. Methods

2.1. Data gathering

We obtained plans by: (1) broadcasting requests for CCPs to members of the IUCN's Connectivity Conservation Specialist Group (498 email addresses) and to subscribers and Twitter followers of the website Conservation Corridor (2018); (2) searching for plans online; and (3) asking colleagues around the world to provide us with any CCPs they were aware of, search the internet for CCPs in their own language, and reach out to their contacts for additional CCPs. To qualify as a CCP for our review, a document must have been written to guide land use decisions, acquisition of conservation lands, construction of highway crossing structures, development of law or policy, or other actions to conserve or improve animal movement, gene flow, or other types of ecological connectivity. One of us (TC or RJ) categorized each document as a CCP, not a CCP, or questionable. PB or AK provided a second opinion for documents in the second and third categories, sometimes followed by brief discussion. In several instances we recognized that two documents were part of a single CCP. The list of 263 CCPs included in the final sample is available in appendix S-1 is available online at stacks.iop.org/ERL/14/103001/mmedia; the CCP documents are available at Conservation Corridor (2018).

We asked the lead author of each CCP to complete an online survey about partners involved in writing and funding the plan, plan objectives, study landscape attributes, data and models used for plan development, and actions recommended in the plan (see appendix S-2 for full survey questions). We asked each person who wrote multiple plans (up to 17 plans per author) to select and complete surveys for two plans that were most representative of their overall body of work. We sent up to two follow-up requests to non-responding authors. During survey development, three of us (PB, AK, TC) independently completed surveys for four plans and examined agreement among our responses, revising survey questions as needed to make them unambiguous. We cleaned and recoded raw data from the author survey responses to create variables representing key CCP characteristics (appendix S-3, Q1–106) and generated new variables by combining survey responses and creating new composite categories as needed (appendix S-3). We received a total of 109 survey responses.

To obtain additional information about the development and implementation of CCPs, we conducted phone interviews with 77 willing authors and/or implementers recommended by authors. We only interviewed persons associated with plans released in or before 2016 to allow time for implementation of plans to have occurred. We asked a standard set of questions (appendix S-4) about the extent to which the CCP informed efforts to conserve connectivity, how plan developers interacted with potential implementers during or after plan development, and factors that promoted or impeded implementation. We used audio recordings of the interviews to create written summaries and extract quotes. Survey and interview protocols were approved by the Committee for Protection of Human Subjects of Northern Arizona University (permit 1185210-1).

2.2. Data analysis

We summarized all 263 CCPs by date and nation. We used cluster analysis to characterize variation among 109 CCPs for which authors completed questionnaires. This resulted in four sets of clusters of CCPs: one set of clusters related to types of institutions involved, another set of clusters related to the spatial scale of the plan, a third set related to plan objectives, and a final set related to recommended actions. The CCP traits used to define each set of clusters are listed in appendix S-6. Because most of these CCP traits were categorical, we used the k-medoids clustering algorithm and Gower's distance metric. For each set of clusters, we identified the number of clusters as the number beyond which there was little marginal decrease in the mean distance to cluster centroid, using the cluster package for R (Maechler *et al* 2018) and the fpc package for R (Hennig 2018). We used the cluster analysis only for description, not as predictors of implementation outcomes.

We used multiple statistical approaches to identify meaningful relationships between plan characteristics (predictor variables; appendix S-5) and the implementation outcomes (response variables; table 2 and appendix S-5). We measured the strength of association between implementation outcomes and categorical predictor variables (all but one of our potential predictors) by calculating Cramer's V, a metric that is independent of sample size and is generalizable across contingency tables of varying size, for each pair of predictor and response variables. For predictor variables with non-mutually exclusive levels (e.g. one plan could have multiple funder types), we created a binary variable for each level of the variable. We considered any plan characteristic with $V > 0.3$ as a potentially meaningful predictor of the associated implementation outcome (Cohen 1988). We used logistic regression to test for associations between plan age (i.e. number of years since publication; our sole continuous predictor) and implementation outcomes. For each implementation action, we also calculated an implementation rate (i.e. the proportion of CCPs that resulted in that implementation occurring). We calculated implementation rates separately for CCPs that explicitly recommended that implementation action, and for CCPs that did not include such a recommendation.

Two of us (KJ and GS) coded the interview responses using NVivo software (coding schema in appendix 3–4). We tested for inter-coder consistency across two comparison cases and had above 90% reliability across all themes. Our deductive thematic coding included six broad thematic categories that we expected to influence implementation of CCPs: (1) engagement with partners in the planning process; (2) leadership in the planning process; (3) implementation actions; (4) communication with external society; (5) drivers of implementation; and (6) barriers to implementation. During the analysis, we added subthemes and eventually reorganized and renamed subthemes, following the abductive approach common in qualitative thematic coding in which emergent themes are added to the existing deductive coding schema (appendix S-3; Gibbs 2018). We used interview coding to create a set of quantitative variables that characterize various aspects of the plans, including those related to partner engagement, leadership style, and implementation actions. All variables derived from the qualitative data are included in the full codebook (appendix S-3, N1-N29).

3. Results

3.1. Descriptive statistics

We collected 382 documents of which 263 qualified as distinct CCPs. The earliest plan was from 1990, with 11 plans released during the 1990s, 89 during 2000–2009, and 163 since 2010. One hundred thirty-two plans were from North America, 50 from Europe, 40 from Africa, 23 from Asia, 13 from South America, and 5 from Oceania (figure 1).

Of 228 requests to authors, 109 resulted in completed online surveys (48% response rate), of which 97 plans were published in or before 2016. Authors of 77 of the 97 plans agreed to be interviewed (79% response rate). Of the 109 plans scored in the online survey, 52 were from North America, 25 from Europe, 14 from Africa, 8 from Asia, 7 from South America, and 3 from Oceania (appendix S-6). Of these 109 plans, we identified 49 as 'shovel-ready' plans and 60 as 'vision' plans. We defined a shovel-ready plan as a CCP that

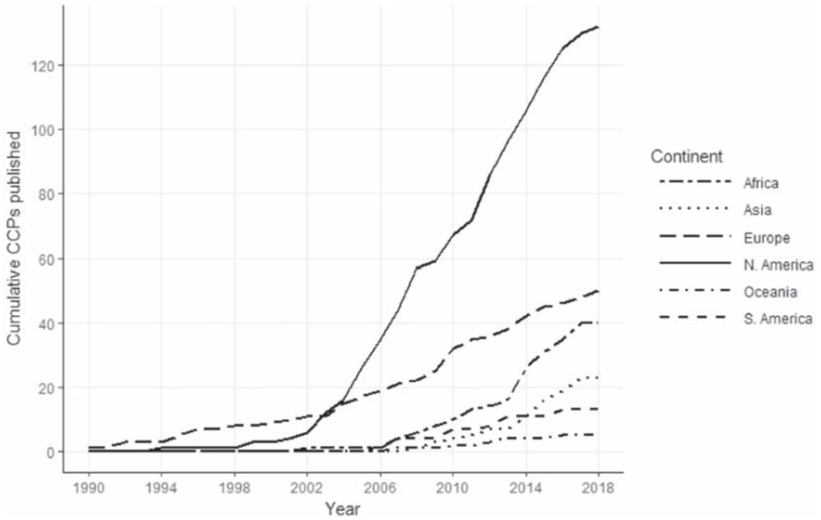


Figure 1. Minimum cumulative number of 263 connectivity conservation plans (CCPs) published between 1990 and 2018. Although we did not discover all CCPs, the graph likely reflects temporal trends on each continent.

recommends protecting specific areas in enough detail that an implementer could select particular parcels for protection, or recommends building a particular type of wildlife overpass at a specific location, or recommends restoring native vegetation in a specific area (Beier *et al* 2008). We defined a vision plan as a regional-scale CCP intended to serve as a vision map or a decision support tool for a connected landscape, put connectivity on the radar of decision-makers, or inspire future conservation actions, including development of shovel-ready plans (Beier *et al* 2011). The vision plans tended to have larger spatial extents and greater numbers of corridors than shovel-ready plans, but there was considerable overlap between the two types of CCPs in these two attributes (figure 2).

Of the first authors of plans, 42 listed their primary affiliation as an NGO, 30 as a government agency, 28 as an academic institution, 7 as consultants, and two as 'other.' About half (57 of 109) of the CCPs were written for regions that had a law or policy requiring or recommending conservation of corridors or connectivity. Threatened and endangered species were included as focal species in at least 60 CCPs that were designed to facilitate movement or gene flow of focal species. At least one face-to-face meeting between authors and some of the stakeholders and end-users occurred during the development of 94 of 109 CCPs. More than half (28 of 49) of shovel-ready CCPs provided detailed plans for areas that had previously been identified in a vision plan as high-priority areas for connectivity conservation.

The cluster analysis yielded reasonably well-fitting results (table 1; see appendix S-7 for full results). In the institutional leadership dimension, for example, there was a distinct cluster of 'big tent' plans, which included high diversity of types of partners and funding sources, and that were usually led by an NGO. Another cluster tended to be led by academics and funded by government. In the spatial type dimension nearly half the CCPs had many corridors and covered large planning areas. The set of clusters defined by CCP objectives was fairly evenly split among designing corridors for a single mammalian species (typically a carnivore), designing for structural connectivity, and a mixed approach taking focal species, structural connectivity, and non-connectivity objectives into account. In terms of the types of recommended actions, most plans included a variety of recommendations; more narrowly focused plans tended to identify policy and planning as appropriate implementation recommendations. Sixteen plans made no specific implementation recommendations, 11 of which were vision plans.

3.2. Relationships between CCP characteristics and implementation outcomes

All 77 CCPs were followed by at least one type of implementation activity, sometimes including actions that were not specifically recommended in the plan. The five main types of implementation actions were: (1) wildlife crossing structures across highways, (2) ecological restoration of degraded areas, (3) land purchases or easements, (4) recognition of corridors through zoning or government designation, and (5) public engagement in connectivity planning and advocacy. In this section, we summarize how these five types of implementation were related to CCP traits; this is followed by insights into important conditions and traits that emerged during the interviews.

3.2.1. Association of implementation outcomes with CCP traits

Table 2 shows how each of the five implementation outcomes was quantitatively associated with one or more CCP traits (see also appendix S-8). Four traits affected the likelihood that crossing structures would be built. One such trait was location: crossing

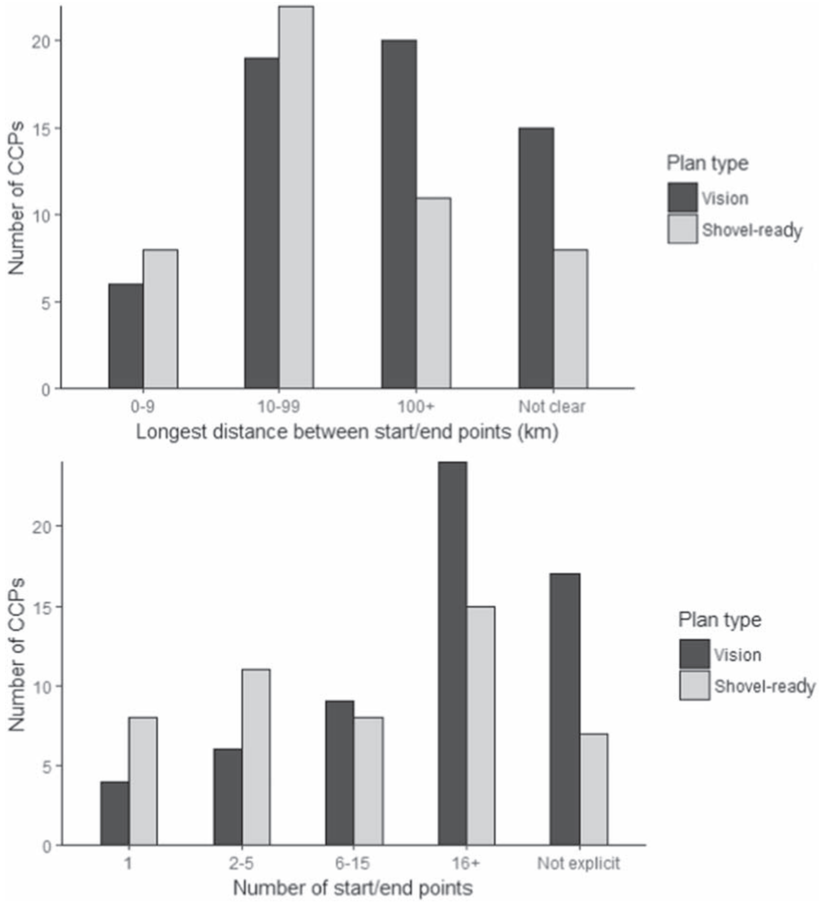


Figure 2. Relationship between plan type ('vision' versus 'shovel-ready') and longest distance between start and end points (top panel) or number of pairs of start and end points (bottom panel) for 109 connectivity conservation plans.

Table 1. Four sets of clusters for 109 connectivity conservation plans.

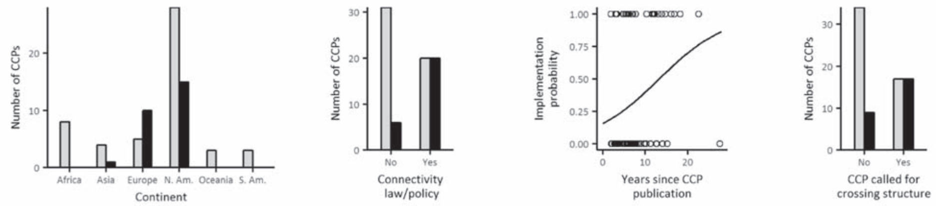
Cluster set	Clusters	Number of plans
Institutional Leadership[a]	*Led by academics, funded by government*	36
	NGO	23
	Government	29
	High diversity of types of partners and funders; usually led by an NGO	21
Spatial[b]	*Many corridors, and longest distance between start/end points > 100 km*	47
	Few start/end points, and longest distance between start/end points 10–99 km	27
	No explicit start/end points	35
Objectives[c]	*Charismatic species connectivity*	31
	Structural connectivity	37
	Charismatic species, structural connectivity, and non-connectivity objectives	41
Recommended actions[d]	*Only planning and policy*	24
	Planning and policy, and physical landscape alterations	38
	Planning and policy, public education, and physical landscape alterations	31
	No concrete recommendations	16

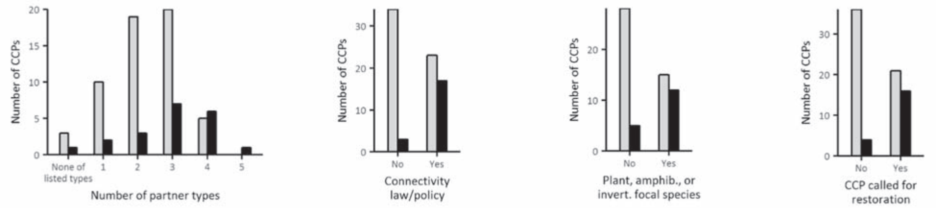
[a] Mean distance between clusters: 0.473. Mean distance with clusters: 0.254. Mean silhouette width: 0.323.
[b] Mean distance between clusters: 0.811. Mean distance within clusters: 0.539. Mean silhouette width: 0.281.
[c] Mean distance between clusters: 0.520. Mean distance within clusters: 0.319. Mean silhouette width: 0.309.
[d] Mean distance between clusters: 0.541. Mean distance within clusters: 0.061. Mean silhouette width: 0.827.

structures followed 67% of European CCPs, but less than 35% of CCPs elsewhere, and in locations with connectivity laws or policies, 50% of CCPs resulted in crossing structures, compared to 16% of CCPs leading to crossing structures in places without connectivity laws. There was a positive association between time since the CCP was released and the likelihood of crossing structures being built, and a higher implementation rate (50%) for crossing structures when the CCP called for crossing structures, compared to 21%

Table 2. Five actions resulting from 77 connectivity conservation plans (CCPs), and CCP traits affecting whether the action was implemented. This table concerns only those traits that were assessed across all 77 CCPs and which therefore could be statistically analyzed; the text describes the influence of traits that emerged from interviews.

<table>
<tr><th>Action</th><th>Plan traits associated with implementation, and type of association.</th></tr>
<tr><td>Construction of crossing structures

Crossing structures implemented
No
Yes</td><td>
</td></tr>
<tr><td>Ecological restoration

Ecological restoration implemented
No
Yes</td><td>
</td></tr>
<tr><td>Land purchase or easement

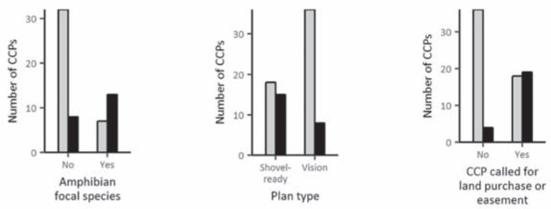
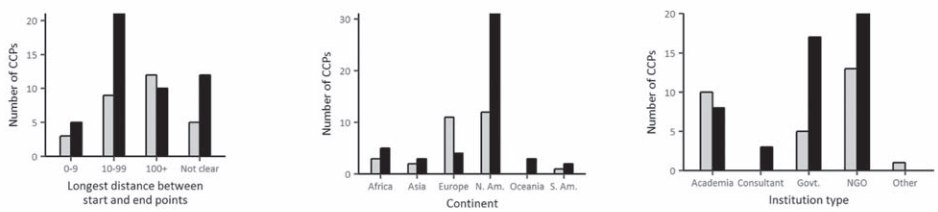
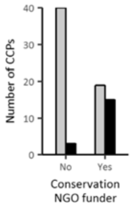
Land purchase or easement implemented
No
Yes</td><td>
</td></tr>
<tr><td>Recognition of corridors through zoning or government designation[a]</td><td>
</td></tr>
</table>

Table 2. (Continued.)

Zoning or designation implemented No Yes	
Public outreach & education[b] Public outreach or education implemented No Yes	

[a] Implementation rate did not differ between plans recommending zoning or government designation (30/50 = 60%) versus CCPs without such recommendation (18/27 = 67%).

[b] Implementation rate did not differ between plans recommending outreach (7/28 = 25%) versus CCPs without such recommendation (11/49 = 22%).

in CCPs that did not specifically call for crossing structures. In interviews, plan authors noted that in at least two US states (Arizona and California), the state transportation agency was a primary sponsor of statewide vision plans that identified corridors based on ecological integrity (rather than focal species). In each state, shovel-ready plans, each using focal species to define linkages, were subsequently developed for specific linkages identified in the vision plans; these plans led to the construction of crossing structures or transportation agency plans to build structures during the next major project on the relevant highway.

Ecological restoration was more likely to be undertaken when amphibians, invertebrates, or plants were identified as focal species (for 44% of the plans versus for 15% of the plans when other taxa were focal species), when connectivity laws or policies were in place (for 43% of the plans versus 8% of plans when there were no connectivity laws or policies), and when several different types of partners (e.g. agencies, NGOs, academia) were engaged in CCP development compared to only one or a few types of partners. Land purchases or easements were more likely when amphibians were identified as focal species (65%) than when other taxa drove corridor design (20%), and when the CCP was a shovel-ready plan (45%) instead of a vision plan (18%). Recognition of corridors through zoning or government designation was more likely in North America than on other continents, more likely for CCPs written by government or NGO authors, and less likely for corridors longer than 100 km. Public outreach was a more likely outcome when CCPs were funded by NGOs.

3.2.2. Important conditions and traits of CCPs

In addition to the quantitative relationships illustrated in table 2, other factors affecting implementation of CCPs emerged during qualitative thematic coding and analysis of our interviews. In the following paragraphs, italicized text in quotation marks indicates an interviewee's words.

3.2.2.1. Initial buy-in from key government stakeholder

Many authors and implementers of CCPs led by NGOs or academics emphasized the importance of getting a government agency (specifically a transportation, land-use planning, or regulatory agency) to request that the CCP be developed. In many cases, implementation occurred even when this initial buy-in was not followed by government participation in any other aspect of CCP development. For example, in the Massachusetts Critical Linkages (a coarse vision map) and the Western Massachusetts linkage design (a shovel-ready plan), the state wildlife and transportation agencies requested a science-based CCP. The transportation agency was motivated less by a desire to conserve connectivity than by their need for scientific analysis to help them respond to requests to build expensive highway crossing structures, many of which they feared would be '*wildlife bridges to nowhere*.' The transportation agency enthusiastically provided funding, did not participate in CCP development, and fully endorsed the product. Similarly, Tanzania's national wildlife agency commissioned a university investigator to develop a connectivity plan, but the government did not participate in plan development except to provide permits and other logistical support. In contrast, an NGO author of a US regional vision plan that lacked initial government buy-in lamented the lack of implementation and wished they had tried to '*engage agency staff from the start so it is more their project than our NGO's project*.'

3.2.2.2. The power of vision plans

One of the main results of vision plans was to get connectivity on the radar of transportation and land-planning agencies. One interviewee (an engineer at a transportation agency that co-sponsored the vision plan) stated that before the plan, his agency would look for opportunities to build fences to stop collisions with vehicles, which also stop wildlife movement. If engineers were concerned about wildlife movement, they just '*sat in a room wondering what to do and how to sell the idea to our bosses*.' With the CCP they '*can point to the map and the species list*,' identify opportunities to improve connectivity, and regularly get traction '*up the chain of command*.' In this light, it is not entirely surprising that authors and implementers reported that vision plans sometimes stimulated implementation actions that had not been specifically called for in the CCP.

3.2.2.3. Stakeholder involvement beyond initial buy-in

Almost all shovel-ready CCPs and about half the vision-CCPs interviewees mentioned the importance of stakeholder participation in two key planning stages. First, early in the process, it helped to have stakeholders (not only government agencies, but all parties with local knowledge or interest) suggest and agree on the focal species and boundaries of the habitat cores to be connected. Second, many interviewees mentioned that stakeholder comments on the penultimate draft led to changes that facilitated implementation: '*[It's important to] hold… those targeted implementation meetings where you really ask and try to find out what those specific challenges and opportunities are—because those are the people who really know*.'

However, very few CCPs were fully co-produced with end users. Co-production (Nel *et al* 2016, Beier *et al* 2017) involves stakeholders working with scientists to develop the work plan, choose models and data, specify the format of the outputs, and write guidance on how the CCP should be used in specific decision contexts. Based on the authors' past experience that co-production positively affects implementation, we designed two interview questions to elicit relevant information. To our surprise, only a handful of CCPs used a full co-production model; those interviewees believed that co-production helped. However, none of the other interviewees expressed the opinion that co-production (beyond initial buy-in and review of the penultimate draft) would have enhanced implementation.

3.2.2.4. Staff turnover

Many interviewees stated that staff turnover, especially in transportation agencies and county land use planning agencies, led to a lack of institutional memory and commitment, especially after the loss of a key champion. Conservation NGOs do a better job of staying on mission not only during internal staff turnover but also when staff turnover occurs in other partners. One interviewee (a government staffer nearing retirement) expected that her successor might not want to continue aggressively pushing CCP implementation at first but that NGO staffers would quickly 'educate' her successor. Another government staffer said '*As an agency, we can take this a lot of places, but we don't have the staff to [monitor all of the opportunities] …Thankfully I have [NGOs and community activists] who tell me where I need to show up*.' Turnover in elected officials and program officers in funding agencies can also affect political and financial support for implementation. For example, one respondent noted that implementation of a CCP in the US was '*related to the support of the counties when it comes to easements and acquisitions…[and that] varies with elections*.'

3.2.2.5. Competing land use and uncertain land tenure

In general, the most challenging competing land uses mentioned by respondents were residential and commercial development and transportation and energy infrastructure. Many corridors crossed private lands, making implementation difficult because either land acquisition was expensive, or lack of public support or trust prevented landowners from engaging with connectivity conservation efforts. In other cases, this issue was compounded by land tenure issues; for example, one author of an Asian CCP stated, '*We haven't been able to work with local communities because it is totally unclear who owns what land, whether certain areas are owned by the government or owned by local villages, or what*.'

3.2.2.6. Use of transparent and repeatable procedures

Although implementation did not depend on connectivity modeling methods and underlying data (see next paragraph), many interviewees emphasized that implementation did require that the CCP use the best available data in a transparent, repeatable procedure. One vision plan was developed with extensive public participation but was seen as just a '*wish list of the participants...wanting connectivity near their homes or favorite natural areas...without objective criteria for importance. So, the report as a whole does not have much traction... I think the time would be better spent starting from scientific, well-grounded [linkage designs] and then moving into negotiation and compromises*.' In contrast, plans that used consistent, transparent procedures did gain traction. One implementer (a conservation activist working in an urban area with massive development pressure) reported '*When [before the CCP] I worked on the Regional Transportation Authority's citizens committee, it was filled with car dealers and Chambers of Commerce, and when I proposed these wildlife overpasses... people looked at me like I was from Mars… Having the [shovel-ready CCP] made all the difference in the world*,' resulting in construction of the two large crossing structures, and the corridor planned as conserved open space in county and city land use plans.

We found no statistical or anecdotal evidence that implementation was influenced by the type of connectivity model (e.g. least cost path, expert opinion,

Box 1. Connectivity Conservation Planning in the United States.

Although the United States has no national CCP, at least 120 CCPs have been developed there. In 2002, Congress began funding the State Wildlife Grants program which required each state wildlife agency to develop a State Wildlife Action Plan (SWAP); although SWAPs are not required to address connectivity, several states have developed statewide CCPs, including Florida, California, Arizona, and Washington. Several multi-state CCPs have also been developed, most notably the Staying Connective Initiative, a consortium of many governmental and non-governmental agencies and coordinated by The Nature Conservancy, which encompasses five northeastern states and three Canadian provinces. Another one is the Southeastern Ecological Framework, which covers eight states (Carr *et al* 2002). The US Forest Service Planning Rules (2012) require connectivity planning within individual national forests, including consideration of 'the broader landscape influenced by the plan area' (Rules §219.8). The planning rules provide little guidance on how to accomplish the task, and it remains to be seen how connectivity will be considered in revision of Forest Plans. In addition to strong leadership by states and conservation NGO's, CCP development has also been influence by strong leaders from academia, the federal Climate Adaptation Science Centers, and Landscape Conservation Cooperatives.

Some of the best-implemented US CCPs were developed as components of Natural Community Conservation Plans (NCCPs) in California. Under California's NCCP Act of 1991, a county, city, or regional joint power authority can allow various entities (typically real estate developers or farmers) to destroy some habitat of threatened or endangered species (or species likely to be listed as threatened) in exchange for actions that will have a strong positive net contribution to recovery of those species (through conservation or restoration activities). The development of each NCCP is paid for by developers, but is subject to extensive scientific and public review and final approval by state and federal wildlife agencies. This model incentivizes both developers and conservationist to collaborate on a win–win solution (the NCCP) and abandon the previous pattern of protracted battles over each development project with no certainty of success for either goal. NCCPs are more detailed than other US CCPs, and their implementation steps (written into the NCCP) are more comprehensive, including well-funded efforts to collect baseline data, carry out restoration activities, and monitor response of focal species, an explicit timeline (typically 50 years, reflecting a pay-as-you-go model in which development funds conservation), and permanent full-time staff to oversee the activities. In contrast to the strong NCCP partnership, an interviewee with an NGO-led partnership commented that '*the partnership is everybody's partnership and nobody's partnership at the same time. Each partner has its own funding priorities, and sometimes perceives that submitting proposals on behalf of [the partnership] would put [their entity] it in competition with itself… Good things do happen, but the incentives to cooperate are not as strong as we need them to be*.'

circuit theory, individual-based movement model, climate model). Similarly, there was no statistical evidence that the type of data used to parameterize those models (expert opinion, observed animal paths, road kill locations, camera trap data, gene flow, radio-telemetry) influenced implementation. However, several interviewees remarked that stakeholders were most readily engaged by direct observations such as maps of paths of radio-tagged animals in the planning area or maps of clusters of road-killed animals. A single animal movement path in the project area could be more compelling than the output of the most sophisticated model based on masses of genetic data collected in the project area or masses of movement patterns observed elsewhere.

4. Discussion

The sheer number of CCPs we gathered (263) is an impressive body of work to have accumulated over the 30 years since the first plan was published, especially considering that many CCPs doubtless escaped our attention, especially those written in less common languages without English translation. Perhaps the most impressive descriptive statistic is that most plans were followed by implementation actions that promoted connectivity conservation, even when some of those actions were not specifically recommended in the CCP. We acknowledge the point, raised by a few thoughtful interviewees, that it is overly simplistic to assume that a CCP 'caused' every crossing structure or conservation land acquisition called for in the plan. Instead each plan is '*another reason to conserve, and another piece of the puzzle that help people make decisions*.' Indeed, in 1985 (well before the first known US CCP), during construction of a canal in southern Arizona (US) the state wildlife agency persuaded the water authority to acquire and permanently protect a broad swath of land between two mountain ranges and to put the canal into a 1 km underground siphon where it crossed the newly protected parcel (R. Schweinsburg, Arizona Game & Fish Department, pers. comm). Box 1 provides more detail on the history of CCP in the United States.

Since 1990, production of CCPs has increased markedly in all parts of the world. After an early start in Europe in the eighties and beginning of the nineties, a strong acceleration was seen from 1995 on in North America, and from about 2000 on in the other continents, and there is no clear evidence of having reached a plateau (figure 1). This fact, along with evidence that most CCPs are being implemented, is a hopeful trend. In both the US (box 1) and Europe (box 2), as well as in many other nations and regions, there is high-level policy or legislation requiring (for example, in some European countries and the Republic of South Africa) or encouraging (US) conservation plans. In some places, including much of Europe, government agencies are strongly involved or even the primary producers of CCPs. In contrast, in the US, a CCP could be produced by a conservation NGO, a state wildlife agency, a land trust, a state or regional transportation agency, a university lab (funded by the other entities), or a coalition of these entities.

Box 2. Connectivity Conservation Planning in Europe.

Europe has a long tradition of developing CCPs, with the EU Habitats Directive in 1992 being a strong landmark legislative action (European Commission 1992). National connectivity plans had already been written in eastern Europe in former Czechoslovakia and the former Soviet Union, including the Baltic states, with the general objective of landscape ecological stability (Bucek *et al* 1986, 1996, Mander *et al* 1995). In western Europe the first national ecological network was published and decided upon in parliament in the Netherlands in 1990 (Ministry of Agriculture, Nature Management and Fisheries 1990). In countries such as the Czech Republic, Denmark, and The Netherlands, spatial planning for connectivity conservation is regulated in spatial planning and nature conservation legislation (Jongman *et al* 2004). In contrast, decentralized governments like Germany and Spain, regional governments are given wide latitude in spatial planning, with some guidance from federal statutes (Von Haaren and Reich 2006).

After the convention for biological diversity (CBD) conference in Rio de Janeiro the Council of Europe initiated the Pan European Biological and Landscape Diversity Strategy (PEBLDS, Council of Europe *et al* 1996), making a vision plan for the Pan European Ecological Network (PEEN) at European and national levels its first objective. Political support for investing in conservation of biodiversity, including connectivity, has generally increased over time in Europe (Jongman 2015). Building crossing structures depends on the willingness of the transport sector at European, national, and regional levels to participate in joint planning with conservation agencies and provide funding. The European Commission promotes environmentally friendly road planning and green infrastructure through its co-funding programs with the consequence that wildlife bridges are often included in road projects and stream connectivity that was disrupted by roads is restored. Funding for connectivity conservation projects is partly provided by the European Commission and partly by national or regional governments. National funding is usually based on national or regional planning priorities.

Despite a concerted effort to collect CCPs from all continents, we obtained most CCPs from North America and Europe. Although some of this disparity is probably due to language barriers, we believe most of this difference is real. For example, a Chinese colleague searching (at our request) for CCPs written in Chinese reported that China's government and conservation NGOs are more focused on protected areas than connectivity and are not generating demand for CCPs. Furthermore, Chinese conservation biologists are mostly employed in academia where the reward structure incentivizes publishing papers in academic journals. As a result, China generated few CCPs, and most of those were published as academic papers.

Because Australia is a pioneer in all aspects of conservation biology, including connectivity conservation (Saunders and Hobbs 1991), we were surprised not to find more Australian CCPs. The lack of high-level national policy support may partially explain this dearth. Although Australia released a National Wildlife Corridors Plan for public exhibition in 2012, it was put aside by a newly installed government in 2013 and has not been revived by subsequent governments (Robert Debus, pers. comm.).

Outside of the US and Europe, Israel and South Africa provide two additional examples of strong national-level requirements to consider connectivity in spatial planning. The Israel National Rule 35 created a National Planning Authority that has real power to make land use decisions, including the ability to force highway builders to build crossing structures. The Israel Nature and Parks Authority developed a vision on road crossings for wildlife (Shkedy and Sadot 2004). This has resulted in six wildlife crossing structures on highways, cancelation of a proposed industrial development near the protected site Ramat Hanadiv, and regional environmental plans that include ecological connectivity in other regions (Van der Sluis and van Eupen 2013). In South Africa, the National Environmental Management: Biodiversity Act (2004) requires each province to produce a bioregional conservation plan that includes a chapter on connectivity. The provinces in turn require municipalities to identify critical biodiversity areas. Local, municipal, and provincial planners are mandated to consider the bioregional plan when making planning decisions and to justify deviations from the recommendations of the plan. Government agencies use the plan to inform habitat restoration and public works projects and to allow private and communal lands to receive tax rebates and subsidies for good stewardship. The bioregional plans also inform land use planning mandated by the Spatial Planning and Land Use Management Act (2013), which went into effect in 2015 and requires that within five years, each hectare of South Africa needs to be assigned a spatial planning category (rural development, industrial development, conservation, etc; information from interviewees and the National Terrestrial Carbon Sink Assessment 2015).

5. Recommendations

Combining the qualitative and quantitative analysis provided several strong insights into which CCP traits and practices promoted conservation implementation. We identified nine key factors that make for a successful CCP.

5.1. Partnerships, especially those including government, promote implementation

Most of the interviewees emphasized the importance of partnerships to successful CCP implementation. Relevant partners to engage in CCP development depend on land use, land ownership, the legal connectivity framework, and available funding sources. Conservation NGOs can be important players in CCP development and implementation because they can identify connectivity conservation as a priority action, monitor regions for implementation opportunities, pressure public agencies to take action, raise funds from private funders and foundations, focus on coordinating project partners, prioritize outreach, and serve as trusted brokers among diverse stakeholder interests such as private landowners. NGOs may also be more resilient to political changes that come with shifts in governmental power.

Partners can be involved at different stages of the CCP development process. It is most important that a government transportation, land-use planning, or regulatory agency should request the development of a CCP, because these agencies are always key implementers. Co-production is most appropriate for complex, long-term, multi-scale challenges such as adaptation to climate change, where neither scientists nor managers can specify needed science products in advance. We conclude that most CCPs do not rise to that level of complexity and are well-served by 'co-production light' (partner engagement in initial and final stages). The Pan European Ecological Network had this complexity as a multi-year project that covered all European countries, involved over 100 stakeholders, used 14 mammalian focal species and over 80 bird species, and used several spatial national and international databases (Jongman *et al* 2011).

5.2. Continuity of commitment promotes implementation

Staff turnover, especially in government agencies, or the loss of a key champion can cause failure to implement a CCP. The impact of turnover in government agencies can be mitigated by a law or formally-adopted policy that mandates connectivity conservation. Where this is lacking, NGOs can buffer loss of institutional memory by engaging new government staffers and ensure the continuance of implementation.

5.3. Implementation actions are more likely to occur when the plan asks for them

Although 'ask for what you want' is an intuitively obvious recommendation, our review provides strong empirical evidence for this notion. Crossing structures, ecosystem restoration, and land purchase or easements were respectively 2.4 times, 4.3 times, and 5.1 times more likely to occur when a CCP specifically recommended them (table 2, column 2). Involving the agencies ultimately responsible for implementing the CCP at key stages in CCP development helps ensure that the plan will include key recommendations (Beier *et al* 2008, Bay Area Open Space Council 2011).

5.4. Enabling legislation and policy

Connectivity conservation is done most effectively, especially at a regional or national scale, when it is legislatively mandated and tied to funding. The positive effect of legislation can be clearly seen in the Republic of South Africa, where a Biodiversity Act, passed in 2004, mandates every province to develop a biodiversity plan that considers connectivity areas, which are being implemented mainly through zoning at the municipal level and ecological restoration. In Europe, legislation directing connectivity conservation exists at the level of the European Union (e.g. the EU Habitats Directive from 1992 and the European Biodiversity Strategy from 2011) and in many of the individual countries such as Germany (BNatSchG 2002). National connectivity plans are being implemented in many countries such as the Netherlands, Croatia, and France (Jongman 2015). The Natural Community Conservation Act in California (US) enables local planners to develop comprehensive plans for conservation and connectivity, complete with funding mechanisms for monitoring, restoration, and long-term management.

In many countries, laws and policies on transportation, wildlife, and land use planning do not specifically address connectivity conservation. The existing legislation can be amended or new legislation enacted to build a strong legal framework for connectivity conservation (Lausche *et al* 2013). In the absence of mandatory connectivity legislation and policies, as in many of the United States, NGOs play a more prominent role in providing connectivity conservation leadership and funding.

5.5. Science

Scientists have developed a myriad of approaches to planning and prioritizing corridors (Rudnick *et al* 2012, Keeley *et al* 2018a). Implementation of a CCP does not depend on the specific scientific approach, as long as the approach is transparent and repeatable. Although CCPs (especially vision plans) need not be designed around focal species, direct observations of animal movements are a powerful means to engage stakeholders and elicit public support.

5.6. A toolbox for connectivity implementation

Implementation actions in the 77 CCPs we reviewed included new partnership creation, public outreach, fundraising, data collection, corridor identification, training or capacity-building, government action, resisting negative development, new policies or enforcement mechanisms, land zoning or protection, writing follow-up plans, land or easement acquisition, corridor prioritization, crossing structures, restoration, improvements for permeability, and threat mitigation. We hope future CCP developers will view these as a toolbox for moving from connectivity planning to implementation, working with their partners to select the tools most appropriate for their planning region.

5.7. Focal species

Focal species can be important in CCP development for several reasons. The idea that animals need to move from A to B, and that corridors can make this possible, is easily grasped by non-ecologist stakeholders and implementers. Inviting partners to select focal species engages them early in the CCP development. Different types of focal species can promote implementation success. Charismatic and endangered focal species can build support among stakeholders and citizens. Including endangered species as focal species can also motivate agencies to implement a plan. Amphibians, plants, and invertebrates are often helpful focal species to justify restoration. Mobile mammals as well as amphibians that migrate between breeding ground and upland habitat can motivate the building of crossing structures.

Funding

Funding is an essential ingredient to move CCPs from concept to action. Connectivity legislation that provides funds for implementation can result in successful defragmentation at a national (or international) level. Private charitable foundation funds can provide flexibility, but lack of continuity in funding can be a challenge.

Public outreach

Public outreach, especially when conducted as focal media campaigns, can build support for connectivity implementation action. With public pressure, agencies may be more likely to take conservation action.

Connectivity conservation is essential to conserving biodiversity and ecological processes in a world that is undergoing rapid environmental change. This review has identified connectivity conservation plan characteristics that favor implementation. We hope our findings will improve the policy and practice of connectivity conservation and provide a basis for potential measures of success.

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