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## Review Paper

## The current application of ecological connectivity in the design of marine protected areas

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## ABSTRACT

Marine protected areas (MPAs) are an area-based conservation strategy commonly used to safeguard marine biodiversity and ecosystem services. Ecological connectivity governs the exchange of individuals among spatially fragmented habitats and is often highlighted as an important element in the design of MPAs. However, the degree to which measured or modelled representations of connectivity are applied to marine management decisions worldwide remains unclear. We reviewed the scientific and management literature to explore the application of connectivity in MPAs located in six countries or regions with advanced marine spatial planning. Only 11% of the 746 MPAs we examined considered connectivity as an ecological criterion, increasingly so since 2007. Landscape measures such as habitat linkages were used most frequently by managers and genetic and modelling approaches by scientists. Of the MPAs that considered connectivity, 71% were for state marine conservation areas or reserves in California and commonwealth marine reserves in Australia. This pattern indicates substantial geographic bias. We propose that the incorporation of connectivity in conservation planning needs to become more accessible to practitioners and provide four recommendations that together will allow scientists and managers to bridge this gap: 1. determine whether to prioritize connectivity as an ecological criterion, 2. identify the role of an MPA in supporting connectivity, 3. identify the appropriate spatial and temporal scale of connectivity, and 4. improve regional knowledge of connectivity patterns. We also propose a framework to facilitate the communication of metrics and patterns of connectivity between scientists and practitioners to apply the best available information in the design and adaptive management of MPAs and networks of MPAs.

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## 1. Introduction

Marine protected areas (MPAs) are one of the most widely utilized tools to preserve biodiversity and ecosystem services. MPAs have been shown to mitigate against biodiversity loss by promoting the persistence, recovery and growth of populations (Almany et al., 2009; Gaines et al., 2010; Speed et al., 2018). For MPAs to achieve the goal of biodiversity persistence, the protection of community composition and ecological processes governing marine ecosystems must be ensured. However, global and local threats, such as climate-change mediated shifts in temperature, ocean acidity, sea level rise, and invasive species, habitat loss, and pollution may compromise the effectiveness of MPAs (Harley et al., 2006; CBD, 2008; McLeod et al., 2009; Boyd and Hutchins, 2012; Blašković et al., 2017; Bruno et al., 2018; Kaplan et al., 2018). The application of ecological

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## Acronyms

CBD	convention on biological diversity
CMR	commonwealth marine reserve
GBR	great barrier reef
IUCN	International Union for Conservation of Nature
MCZ	marine conservation zone
MPA	marine protected area
MPAn	marine protected area network
NCMPA	nature conservation marine protected area
SMCA	state marine conservation area
SMR	state marine reserves or reserve
UK	United Kingdom
WDPA	world database on protected areas

criteria that support the goal of biodiversity persistence offers one solution to creating more resilient MPAs in the face of accelerated anthropogenic changes. Connectivity is a fundamental ecological process in marine ecosystems that promotes both persistence and recovery of populations through the dispersal of marine life across populations, communities and ecosystems.

According to the definition provided by the International Union for the Conservation of Nature (IUCN), a MPA is “a clearly defined geographical space, recognized, dedicated and managed, through legal or other effective means, to achieve the long-term conservation of nature with associated ecosystem services and cultural values” (Day et al., 2012). In 2010, the Convention on Biological Diversity (CBD) set a target to conserve “10% of coastal and marine areas [through] ecologically representative and well-connected systems of protected areas” by 2020 (CBD, 2010). This goal underscores the importance of having direct, inferential or predictive measures of connectivity among protected areas. Grorud-Colvert et al. (2014) categorized five types of networks of MPAs (MPAn) ranging from ad-hoc (an unplanned collection) to connectivity-based (multiple ecologically connected MPAs) and concluded that many existing MPAn do not meet the definition of a connectivity network.

Connectivity, the extent to which spatially distinct populations, communities, ecosystems, or habitats are linked by the exchange of genes, organisms (propagules, juveniles and adults), nutrients, and energy is considered an important ecological criterion in the design of true MPAn, where the whole is more than the sum of its parts (Botsford et al., 2009; Cowen and Sponaugle, 2009); however, the use of connectivity in designing MPAs globally has been limited (Leslie, 2005; Magris et al., 2014). Other ecological selection criteria, such as representation of species or habitats, often take priority and are used more frequently (Barr and Possingham, 2013; Margules and Pressey, 2000). Even so, there are instances where connectivity can be pivotal in the decision-making process, particularly for MPAs with limited self-recruitment or where the size of the area required to maintain a viable population exceeds the size of the area proposed to receive protection (Marti-Puig et al., 2013). By prioritizing connectivity, there is also potential for both economic and social benefits to occur (e.g. spillover). Existing MPAn that have not incorporated connectivity may be ineffective in achieving persistence and protection of biodiversity (Magris et al., 2018).

Incorporating connectivity into the design of MPAs and MPAn may be challenging because of the complexity of the methods used to estimate and predict connectivity patterns (Thorrold et al., 2002; Botsford et al., 2009; Burgess et al. 2014; Bryan-Brown et al., 2017). There have been several reviews on methods to quantify connectivity and integrate it into MPAn design (Calabrese and Fagan, 2004; Cowen and Sponaugle, 2009; Magris et al., 2016, 2014), mainly focusing on tropical coral reef ecosystems (Almany et al., 2009; Jones et al., 2009; McCook et al., 2009). Recently, Bryan-Brown et al. (2017) summarized the patterns and trends in connectivity research and identified geographical and taxonomic biases. However, recommendations for integrating connectivity in the design of MPAn have not been consistently implemented by practitioners.

There is a gap between the increasing volume in scientific research on connectivity and its integration into marine spatial planning. Managers and scientists both have long recognized the importance of this ecological criterion (Margules and Pressey, 2000; Roberts et al., 2003; Steneck, 2006), but managers do not have access to tools or operational frameworks that may facilitate collaboration between sectors, or they may not be familiar with the underlying ecological and physical processes mediating connections. Additionally, connectivity is not an area-based target as many other ecological criteria such as representation, making it difficult to develop quantitative objectives for marine spatial planning. Differences in the intended audience of peer-reviewed articles compared to reports in the grey literature and management plans also lead to differences in focus, style, and even the definitions of connectivity, making comparisons difficult.

Here, we review research articles published in the peer-reviewed literature and management plans of protected areas to examine whether connectivity was included in the design of MPAs and MPAn in select countries with advanced marine spatial planning. The scope of this study focuses on marine systems and does not address processes that occur at the land-sea interface. We assessed the variation in prioritizing different ecological criteria, both geographically and temporally. Combining information from management plans and peer-reviewed articles allowed us to outline differences in methods and

application of connectivity between the scientific and management sectors. We provide recommendations and suggest a framework for future incorporation of empirical connectivity measurements into designing and monitoring of MPA and MPAn and identify the actors in each step. This review will add to the growing literature on connectivity by demonstrating the gap between connectivity research and application by practitioners and proposing ways to overcome this gap. Our goal is to stimulate a dialogue and collaboration between these two sectors to promote the use of the best available information on considering connectivity during the implementation of MPAs and MPAn.

## 2. Methods

### 2.1. Database acquisition

We determined the methods and metrics used in the scientific literature to measure connectivity by completing searches in the Web of Science (<https://apps.webofknowledge.com>) and Scopus (<https://www.scopus.com>). The search was completed with default search settings and the following set of search terms (\* represents a wild card): ((population\* OR larva\* OR genetic\* OR landscape\* OR seascape\*) connect\*) AND (MPA OR "marine protected area" OR "marine reserve" OR "marine park" OR "marine sanctuary" OR "marine conservation area" OR "marine nature reserve" OR "marine management area" OR "marine national park" OR "coastal reserve" OR "marine and coastal park") AND (monitor\* OR manage\* OR design OR implement OR designat\*). These search terms were selected to capture studies that discussed connectivity for different designations of MPAs. The first set of search terms selected for research on connectivity, while the second set narrowed the search to articles examining connectivity in MPAs. The last set of search terms focused our efforts further on studies examining different stages of planning, i.e. prior to, during, and after designation to capture studies on planning, implementation and monitoring. The searches were completed on November 22, 2017.

The search terms returned 397 studies, excluding duplicates. An abstract review, completed through the online software covidence (<https://www.covidence.org/>), included 307 studies that both (1) discussed or measured demographic, genetic, or landscape connectivity and (2) discussed actionable goals for MPA design or management. Data were extracted from 186 studies, following the full text review using these two inclusion criteria. Studies were analyzed in alphabetical order to prevent systematic biases in the dataset (see details on information extracted from each paper in [Table A1](#)).

We created a database of MPAs based on management plans, government websites and other managing agency documents. We focused on six countries or regions with advanced systematic conservation planning: Australia, California, Canada, France, Hawaii and the United Kingdom (including England, Northern Ireland, Scotland, and Wales) (hereafter, focus areas). We used MPAtlas to compile an initial list of MPAs in the focus areas, and government websites to produce a comprehensive list. The final list of MPAs was confirmed with the World Database on Protected Areas (WDPA) for completeness. We used the definition of a Marine or Coastal Protected Area by the CBD Ad Hoc Technical Expert Group as our criterion for defining a MPA: "any defined area within or adjacent to the marine environment, together with its overlying water and associated flora, fauna and historical and cultural features, which have been reserved by legislation or other effective means, including custom, with the effect that its marine and/or coastal biodiversity enjoys a higher level of protection than its surroundings" (CBD, 2004).

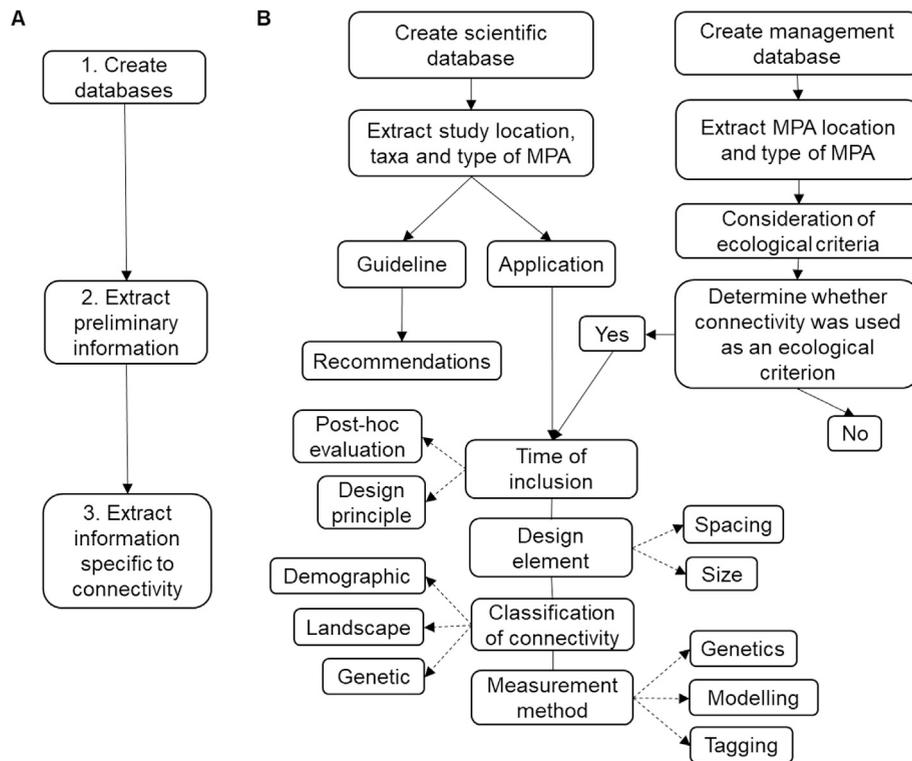
The comprehensive list, generated from management plans, included MPAs that at the time of data assembly were designated (rather than proposed only) (1) legislatively to (2) protect the ecological function, biodiversity, or an oceanographic (physical or geological) feature within an area under (3) a defined managing authority. All three conditions needed to apply for a MPA to be included. Where boundaries or designation types within the study area had changed over time, the most up-to-date regulations and rules were used. Where a new designation had been proposed but not enforced by legislation, the rules of the old designation were used. The final dataset included 746 MPAs and 9 MPAn. Only MPAs designated prior to 31 August 2017 were included in the review. Supplemental information on the information extracted from each MPA and MPAn can be found in [Table A2](#).

### 2.2. Database analysis

The purpose of the scientific and management literature review was to answer two questions: (1) was connectivity used as a guiding principle in the design and evaluation of MPA or MPAn, and (2) if yes, what methods and metrics of connectivity were used by scientists and managers?

#### 2.2.1. Scientific (peer-reviewed literature) database

For the review of scientific literature, we considered studies that explicitly measured connectivity separately from those that only provided guidelines on how to incorporate connectivity in design of MPAs or MPAn ([Fig. 1](#)) (for connectivity categories, see [Fig. 2](#)). For all scientific studies, we extracted the location, studied MPA, and conclusions reached by the study. For studies that explicitly measured connectivity, we also recorded: (1) the study taxa, (2) whether the study was on design or a post-hoc evaluation of planned or existing MPAs, and (3) the methods, metrics and class of measured connectivity (landscape, demographic, and genetic; [Fig. 2](#)). Because protection level varied across jurisdictions and IUCN criteria were not used consistently, we did not include it as a factor in the study. Additionally, the protection of the Commonwealth Marine Reserves (CMR) in Australia changed over the course of the review, with new management plans taking effect on July 1, 2018 (i.e. after we completed our research).



**Fig. 1.** (A). Simplified and (B) detailed flowchart, depicting steps taken to extract information on the inclusion of connectivity in marine protected areas (MPAs) and marine protected area networks (MPAN) from peer-reviewed scientific and management literature. The scientific database consisted of 186 research articles and the management database consisted of management plans for 746 MPAs and 9 MPAN. See section Database acquisition and Database analysis for details.

### 2.2.2. Management database

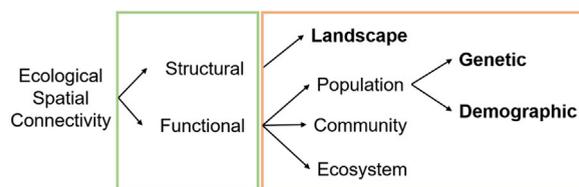
For the review of the management literature, information on location, the category of MPA, managing authority, size of MPA, ecological selection criteria and monitoring strategies were extracted from management plans and websites of governments or other managing agencies for each MPA and MPAN. We considered individual MPAs and MPAN separately since their goals differ. We classified the ecological criteria used in site selection under 14 categories: representative features, areas of high productivity, areas of high biodiversity, biogenic habitats, nursery areas, foraging areas, spawning areas, migratory areas, species at risk, fisheries, complex or unique geomorphology, unique or rare oceanography, culturally important species, and connectivity. For MPAs that used connectivity as an ecological criterion, as well as peer-reviewed scientific articles, we classified connectivity as landscape, demographic or genetic. This allowed us to identify differences in the application of connectivity knowledge between the scientific and management sectors.

## 3. Current state of population connectivity application in research and management

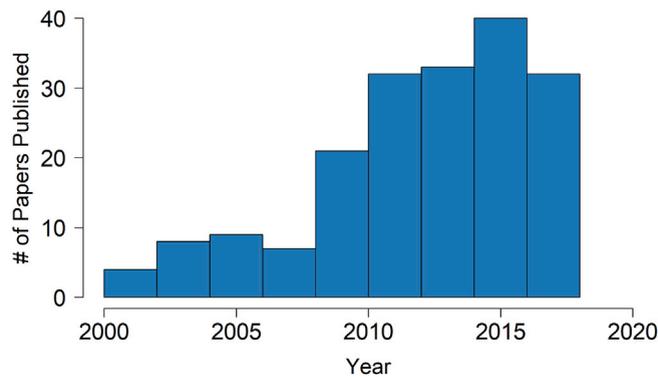
### 3.1. Database summaries

#### 3.1.1. Scientific literature

We identified 38 studies that only provided guidelines (“Guideline studies”) and 148 studies that measured connectivity and, based on their results, made explicit MPA recommendations (“Application studies”; [Table A3](#)). We excluded 37 studies at



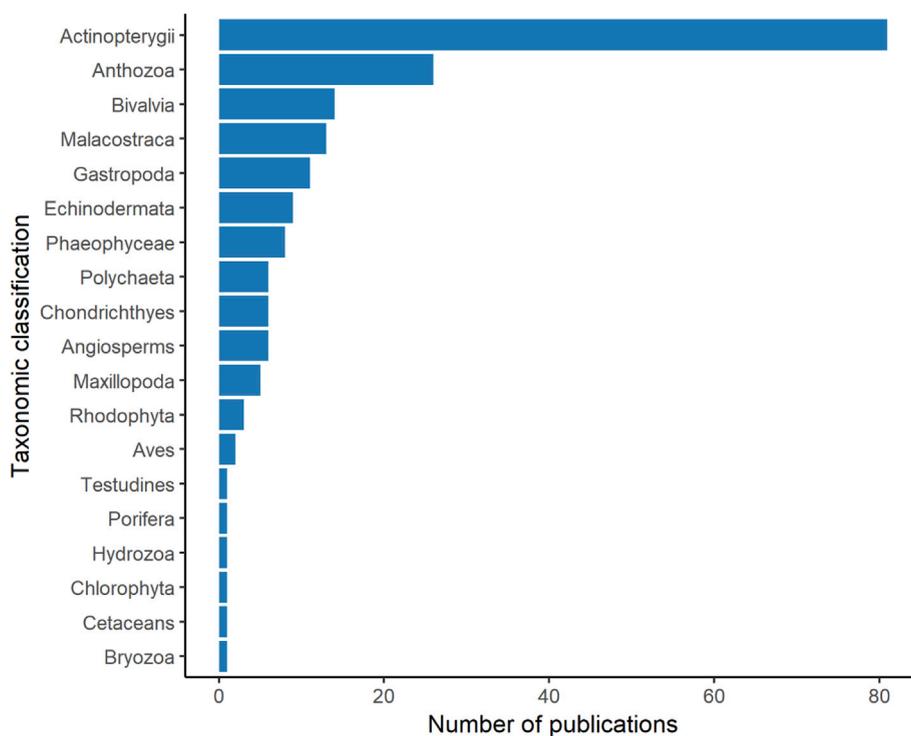
**Fig. 2.** Classification of types of ecological spatial connectivity. Bolded categories are within the scope of this review.



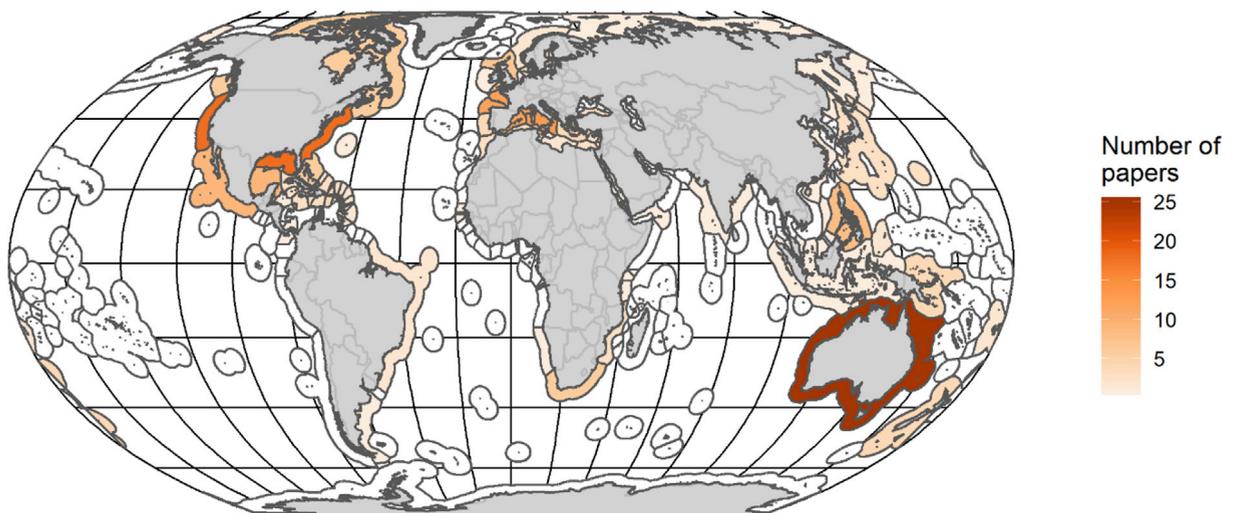
**Fig. 3.** Frequency of publication in the peer-reviewed literature of research articles on the use of connectivity in marine protected areas ( $n = 174$ ). Searches using Web of Science and Scopus were completed on 23 November 2017.

the full-text review stage because, although they stated that their research had MPA applications, they provided no specific recommendations.

Overall, there has been a substantial increase in the frequency of peer-reviewed publications on connectivity in MPAs since 2010 (Fig. 3). These studies focused on a wide range of taxonomic groups but were strongly biased towards ray-finned fishes (Actinopterygii; Fig. 4). Anthozoa were also well studied, followed by Bivalvia and Malacostraca. Of the 148 “Application studies”, 34 focused on MPA design and 122 conducted post-hoc analysis of existing or prospective (area selected but no legislation in place) MPAs. Six studies had elements of analyses for both the design and post-hoc evaluation phases. The 148 studies that measured connectivity focused more often on tropical than temperate areas (Fig. 5). There was a clear geographic bias for research on connectivity in MPAs in Australia and the United States of America (Fig. 5). Notable research efforts on connectivity in MPAs have also focused on the Gulf of California, some Mediterranean countries and the Coral Triangle. Overall, most countries and regions have not been the focus of scientific literature. In contrast, Fig. 5 of Bryan-Brown et al. (2017) indicated that the Caribbean Sea and Northern Europe had the greatest relative research effort in studying marine



**Fig. 4.** Focal taxa used in the peer-reviewed scientific literature on population connectivity in the design of marine protected areas. Taxa are shown in descending order of research effort. Note that each article may focus on more than 1 taxon ( $n = 140$ ).



**Fig. 5.** Geographic patterns in research effort on population connectivity in the design of marine protected areas by country, where colour intensity indicates the number of papers ( $n = 148$ ). Six papers included in the review could not be depicted in this figure: 2 were theoretical models and 4 had an international scope. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

population connectivity. However, we showed that there is minimal application of this research in scientific studies that evaluate connectivity in practice.

### 3.1.2. Management literature

The review of the management literature identified 746 MPAs and 9 MPAn (Table A4). Of the 746 individual MPAs, 80% had clearly defined selection criteria and 47.7% had a management plan, although the criteria were not always stated in the plans. There were 55 categories of MPAs, corresponding to varying levels of protection and legislation types, which reflect different conservation objectives of MPAs. Only 28.2% of analyzed MPAs used the IUCN criteria for levels of protection. Of the identified MPAs, the total area was greatest in Australia (Table 1), which was also where most scientific literature was based.

Representation was the most widely used ecological criterion for siting, followed by areas of high biodiversity and species at risk (Fig. 6). Connectivity was among the least frequently used ecological criteria, followed only by culturally important species (Fig. 6). Conservation of biodiversity was the 2nd most common criterion in Australia and Canada, 3rd in USA (California and Hawaii) and 4th in France and the United Kingdom (UK). Species at risk was the 2nd most common criterion in France and USA, 3rd in Australia and Canada, and not included in the top 5 criteria in the UK. Biogenic habitats were 3rd most commonly used in UK and France, 4th in Australia and the USA, and 5th in Canada. The number of ecological criteria considered for an individual MPA ranged from 1 to 14, with a median of 7.5 (Fig. 7).

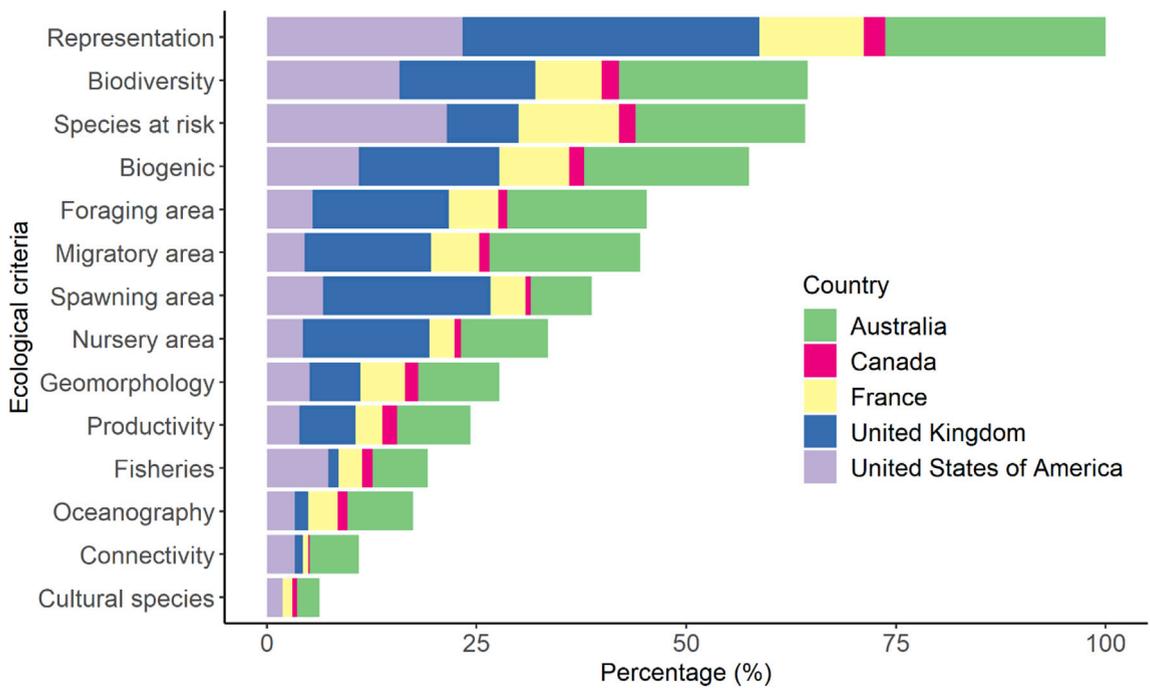
Connectivity was used as an ecological criterion in 11% of MPAs. There has been an increasing number of designations that considered connectivity over time, particularly after 2007, closely mirroring the trend seen in the scientific literature (Fig. 3, Table 2). This is likely related to the development of the strategic plan to “halt the loss of biodiversity” by 2010 at the 6th Convention of Parties of the CBD (CBD, 2002). The frequency of designations that consider connectivity remained high (>20 every 5 years) as 2020 approaches, presumably as countries attempt to reach the Aichi Biodiversity targets.

Of the MPAs that considered connectivity, 70.7% were for state marine conservation areas (SMCA) or reserves (SMR) in California and CMRs in Australia (Table 2). This pattern indicates substantial geographic bias and significant differences in conservation planning and prioritization among countries. These MPAs were all part of MPAn we identified (5 in Australia and 2 in California), suggesting that MPAs designed to be part of networks are more likely to consider connectivity. Of the 9 MPAn, 8 discussed connectivity as part of their network strategy. However, empirical evidence to support that these networks are more than a collection of MPAs was not provided. Additionally, quantitative conservation objectives that address connectivity for focal species at relevant spatial and temporal scales were not stated.

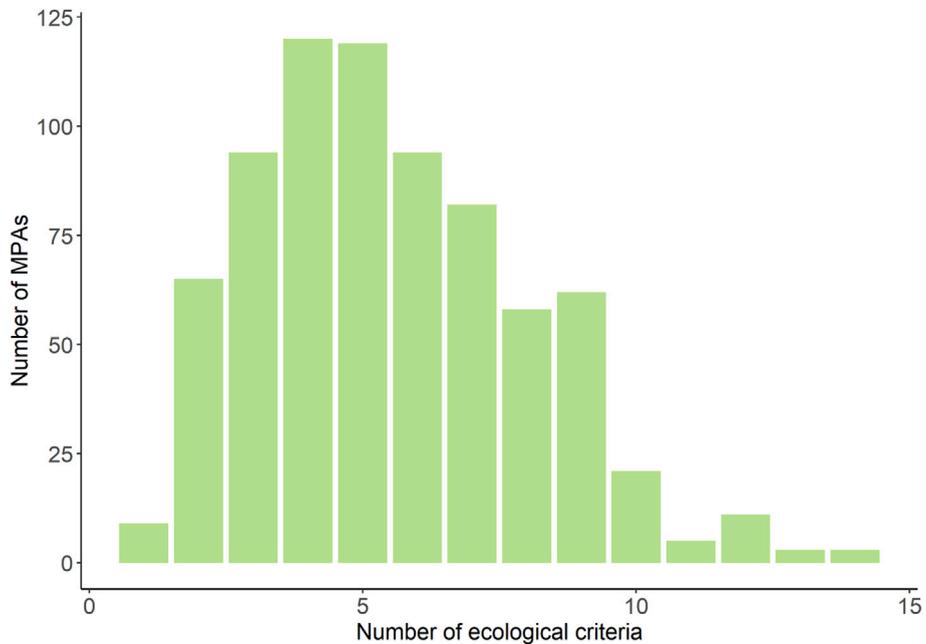
**Table 1**

Number and total marine area ( $\text{km}^2$ ) of marine protected areas (MPAs) and MPA networks analyzed per country.

	Total Marine Area ( $\text{km}^2$ )	Number of MPAs	Number of MPA networks
Canada	184503	19	0
United States of America	1538429	174	2
Australia	3193193	196	5
United Kingdom	114001	265	1
France	42955	91	1



**Fig. 6.** Use of 14 ecological criteria in the design of 746 marine protected areas in Australia, Canada, France, United Kingdom and the United States of America (California and Hawaii only).



**Fig. 7.** Number of ecological criteria considered in the designation of 746 marine protected areas (MPAs) in Australia, Canada, France, United Kingdom, California and Hawaii. Ecological criteria were classified into 14 categories: representative features, areas of high productivity, areas of high biodiversity, biogenic habitats, nursery areas, foraging areas, spawning areas, migratory areas, species at risk, fisheries, complex or unique geomorphology, unique or rare oceanography, culturally important species, and connectivity. Refer to Fig. 6 for details on the use of each ecological criteria.

**Table 2**

Types and years of designation for marine protected areas that included connectivity (USA = United States of America (California and Hawaii only), UK = United Kingdom, MPA = marine protected area).

Type of MPA	Year of designation	Country	Number of MPAs
Aquatic Reserve	1998	Australia	1
Area of Interest	2017	Canada	1
Commonwealth Marine Reserve	1999	Australia	1
Commonwealth Marine Reserve	2007	Australia	13
Commonwealth Marine Reserve	2013	Australia	24
Marine Conservation Zone	2013	UK	1
Marine Conservation Zone	2016	UK	3
Marine National Monument	2006	USA	1
Marine Park	1990	Australia	1
Marine Park	2005	Australia	2
Marine Park	2016	Australia	2
Nation Wildlife Refuge	1972	USA	1
National Marine Sanctuary	1992	USA	1
National Wildlife Refuge	1972	USA	1
National Wildlife Refuge	1988	USA	1
Nature Conservation Marine Protected Area	2014	UK	2
No take zone	2008	UK	1
Parc National	1963	France	1
Parc National	2012	France	1
Parc Naturel Marin	2011	France	1
Parc Naturel Marin	2012	France	1
Parc Naturel Marin	2016	France	1
State Marine Conservation Area	2007	USA	2
State Marine Conservation Area	2010	USA	2
State Marine Conservation Area	2012	USA	5
State Marine Reserve	2007	USA	3
State Marine Reserve	2010	USA	7
State Marine Reserve	2012	USA	1

#### 4. Methods and metrics used to incorporate connectivity into MPA design

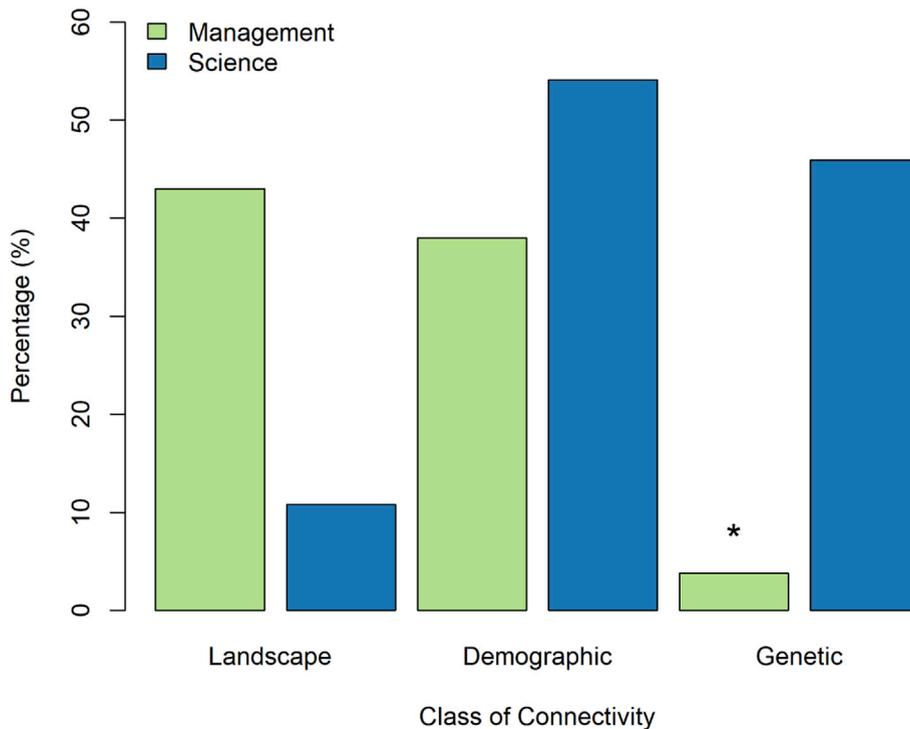
There is no scientific consensus on the most appropriate method to measure connectivity or on the metrics to include in the design process of MPAs. Four methods of measuring connectivity were identified by [Bryan-Brown et al. \(2017\)](#): modelling, tagging, genetics and simple observation. Modelling approaches require complex and specific input, such as fecundity or survival, to calculate metrics such as local retention and evaluate population persistence in MPAN ([Burgess et al., 2012](#)). Genetic approaches are expensive and time-consuming, but provide detailed metrics of genetic structure and diversity of metapopulations on scales of 1 km–100 km ([Beltrán et al., 2017](#)). Both these methods rely on data that may not be available for many MPAN designs or post-hoc evaluations carried out by practitioners.

Depending on the method used to collect connectivity data, various metrics can be used to elucidate connectivity patterns. These metrics can be based on genetics, network analysis, parentage analysis, gradients in biomass and morphometrics, among others ([Bode et al., 2012](#); [Schill et al., 2015](#); [Buchholz-Sørensen and Vella, 2016](#); [Teschima et al., 2016](#); [Williamson et al., 2016](#)). Some of these metrics can only be calculated using certain approaches (e.g. genetic methods to calculate genetic diversity, or connectivity matrices to calculate network metrics such as betweenness centrality). Metrics can also be calculated from proximity of habitats (Euclidean distance) or inferring source populations based on circulation patterns and residence times. Metrics such as local retention, betweenness centrality and outflow are particularly useful to incorporate in MPA design ([Burgess et al., 2014](#); [Magris et al., 2018](#)). Local retention, the proportion of reproductive output that recruits back in the donor population, provides details on replacement and therefore persistence of a population. However, [Burgess et al. \(2014\)](#) identified that self-persistence, the proportion of total recruitment to a population that was produced at that population is often used instead, although it provides no information on persistence.

In the scientific literature, demographic connectivity was studied most often, followed closely by genetic connectivity ([Fig. 8](#)). This is largely different than efforts in the management literature ([Table 3](#)), where landscape connectivity, such as habitat connections, was used most frequently, followed closely by demographic measures ([Fig. 8](#)). Genetic measures were discussed in the management plan of only three MPAs (3.7%; [Fig. 8](#)). Recommendations to overcome these differences are discussed in section 5. Below we summarize the approaches used by scientists and managers, respectively, to measure and apply connectivity.

##### 4.1. Demographic approaches

In the scientific literature, individual-based modelling approaches yielding dispersal trajectories, connectivity matrices (i.e. source distribution matrix) and dispersal kernels were commonly used ([Puckett and Eggleston, 2016](#); [Ross et al., 2017](#); [Rossi et al., 2014](#); [Storlazzi et al., 2017](#)). Some studies tailored metrics to taxa with different spawning and larval traits and



**Fig. 8.** Class of connectivity used in the scientific literature ( $n = 148$ ) and management plans ( $n = 82$ ). Note that interdisciplinary studies may have considered more than one class of connectivity. \*Genetic connectivity in the management literature was discussed only as a summary of known information for that region.

**Table 3**

Examples of connectivity metrics used in the management literature.

Connectivity metric	Example description	Example MPA	Category of MPA
Habitat linkage	Provides linkage to other similar habitats	Runswick Bay, England	Marine Conservation Zone
Larval exchange	Site protected for its role in larval exchange with other marine habitats	San Elijo Lagoon, California, USA	State Marine Conservation Area
Retention	Larval retention zone of regional importance for many fish and invertebrate species	Point Reyes, California, USA	State Marine Reserve
Source	Area considered to be a larval source	Big River Estuary, California, USA	State Marine Conservation Area
Spillover	Increase supply of large adult and larval fish that can disperse to other areas for fisheries harvest outside MPA	Asilomar, California, USA	State Marine Reserve
Stepping stone	An important biological stepping stone facilitating the transport of biological material	Cook Island, Australia	Aquatic Reserve

further combined them in a multi-species approach (Holstein et al., 2014; Schill et al., 2015). Fifteen studies used tagging methods to calculate connectivity metrics (six with electronic tags and nine with natural passive tags), 13 for fish, one for molluscs and one for arthropods. Natural or artificial markers were used to delineate natal origin of captured or recaptured larvae, juveniles and adults in existing MPAs (Gomes et al., 2016; Lazartigues et al., 2016; Di Franco et al., 2012), whereas electronic tags were used to track movement of adults within and among MPAs with acoustic telemetry being particularly useful for large predators (Ponchon et al., 2017; Espinoza et al., 2015).

In the management literature, demographic connectivity was identified through stepping stones, sources, retention zones and areas that provide spillover to adjacent protected or unprotected areas (Table 3). The Big River Estuary, Ten Mile Estuary and Navarro River Estuary SMCA's in California and the North-west Orkney and Turbot Bank nature conservation marine protected area (NCMPA's) in the UK were identified as larval sources. The Asilomar SMR, Calanques National Park, Golfe du Lion Natural Marine Park, Fylde marine conservation zone (MCZ) and Lamlash Bay no-take zone benefit adjacent fished areas through spillover of adults.

#### 4.2. Landscape or seascape approaches

In the scientific literature, habitat modelling was used in scenarios with limited data on spatial distribution that can still provide some information on habitat linkages to managers (Anadón et al., 2011; Engelhard et al., 2017). For example, in the

Baltic Sea, analysis of ecological coherence (representation and connectivity) using landscape measures was used to evaluate existing MPAn in areas where modelling or genetic data were not available (Sundblad et al., 2011; Jacobi et al., 2012). Landscape surrogates, such as patterns of reproductive output or the protection of high-density and extensive habitat provided details on larval subsidy when empirical evidence was limited (Schmiing et al., 2017; Shackell et al., 2013), and was proposed to increase fishery harvests (Bode et al., 2012).

In the management literature, landscape connectivity often related to habitat linkages. For the 5 networks of CMR and the Coral Sea CMR in Australia that cover the offshore regions, management plans discussed connecting habitat to coastal Marine Parks (Director of National Parks, 2013; 2017a, 2017b; 2017c, 2017d, 2017e). Similarly, the Western Channel MCZ was deemed important for connecting both offshore MPAs within the UK and to MPAs in France's exclusive economic zone (JNCC, 2016a). The Hartland Point to Tintagel MCZ is considered critical for connectivity of habitats in the area, contributing to the protection of large intertidal habitats (JNCC, 2016b).

#### 4.3. Genetic approaches

Genetic methods for measuring connectivity have become increasingly more common since 2005 (Bryan-Brown et al., 2017). In the scientific literature, 68 of 148 studies utilized genetic approaches, 16.2% to inform the design of new MPAs and 95.6% in post hoc analyses for existing MPAs (8 studies had elements of design and post-hoc analyses). Genetic metrics of isolation by distance, gene flow, population structure and haplotype diversity by genetic clustering have been used to discern connectivity patterns in MPAs (Cossu et al., 2017; Wright et al., 2015; Holland et al., 2017; Sandoval-Castillo and Beheregaray, 2015; Matias et al., 2013). There are multiple types of genetic approaches that can address different scientific questions related to dispersal, source or origin of individuals and population structure (Manel et al., 2005). For example, many papers asserted that populations with measurable genetic structure at fine spatial scales ( $\leq 100$  km) require small, moderately spaced MPAs to increase genetic connectivity through stepping stones (Shanks et al., 2003; McCook et al., 2010; Wright et al., 2015). Further details on the calculation of genetic connectivity metrics or an overview of genetic assignment methods can be found in Manel et al. (2005), Selkoe et al. (2016) and Bryan-Brown et al. (2017).

Genetic methods were not discussed with respect to design in the management literature. However, the management plans of three MPAs in Hawaii (Papahānaumokuākea Marine National Monument, Midway Atoll National Wildlife Refuge, and the Hawaiian Islands Humpback Whale National Marine Sanctuary) summarized genetic connectivity measurements as part of ongoing research, highlighting the advantages of a holistic view of the ecological structure in protecting resources in these areas ("Papahānaumokuākea Marine National Monument Management Plan," 2008; Chow et al., 2015). For the Humpback Whale National Marine Sanctuary, a summary of completed connectivity research suggests that species are well-connected between Ni'ihau, Kaua'i and the Northwestern Hawaiian Islands (Toonen et al., 2011).

#### 4.4. Connectivity surrogates

In cases where quantitative approaches are not feasible, rules of thumb can be used instead; however, these are less reliable than the approaches discussed above. These rules may be informed by ecological life history characteristics, such as planktonic larval duration of focal species, and environmental characteristics, such as magnitude and direction of currents or temperature (Burt et al., 2014; D'Aloia et al., 2017; Smith and Metaxas, 2018; but see Bode et al., 2016). Oftentimes, surrogates for connectivity are used to determine size and spacing of reserves, stepping stones and clustering (Airamé et al., 2003; Moffitt et al., 2011). However, Bode et al. (2016) suggest that using quantitative rules of thumb, ranking habitat patches and using subsets of data (e.g. self-recruiting proportion) are inadequate methods for incorporating connectivity into MPA design. Since these approaches measure an explicit demographic process, they require a post-hoc assessment to evaluate persistence (e.g. population viability analysis) (Bode et al., 2016).

Rules of thumb should not be used in place of empirical or derived measures of connectivity because they rarely elucidate species-specific patterns or represent the entire process of connectivity. The process of connectivity comprises various ecological events including reproductive output, dispersal, settlement, post-settlement survival (recruitment) and reproduction (reproductive population connectivity) (Pineda et al., 2007). Species-specific differences in the characteristics that are incorporated into rules of thumb (e.g. pelagic duration, home range, and reproductive timing) may prevent the application of these rules at the network scale because size and spacing guidelines may produce contrasting results for different species. Lastly, most rules of thumb to guide size and spacing of MPAs have been developed for well-studied taxa such as fish and coral reef ecosystems, respectively, and practitioners should exercise caution when considering these guidelines in ecosystems with different spatial structures (e.g. temperate or polar systems).

#### 4.5. Combining approaches

All approaches that quantify connectivity have limitations. For example, biophysical models are limited in resolution and scale because of computational constraints. It is difficult to select a scale that is both accurate in representing dispersal dynamics and computationally efficient, because the physical processes affecting larval transport vary from large- (e.g. gyre movement) to small-scale processes (e.g. eddies). Genetic approaches, more specifically assignment tests, assume that all potential source populations are sampled and in Hardy-Weinberg equilibrium (Manel et al., 2005). Tagging methods have

only been applied to larger organisms, mainly fish. Whenever connectivity is estimated, empirical data are needed to test the assumptions of models and validate their outputs. A robust assessment of connectivity should compare outcomes from multiple metrics and approaches. To address this, cross-validating studies using multiple methods to measure connectivity patterns have been proposed for a single system (Palumbi, 2003; McCook et al., 2009).

## 5. Recommendations for incorporating connectivity in the design of MPAs

The scientific literature contains numerous suggestions on how to incorporate population connectivity into the design and adaptive management of specific MPAs and MPAn. There are examples of MPAs implementing these suggestions in the design and post-hoc evaluations of management decisions. The inclusion and prioritization of connectivity in the design of MPAs depends on conservation objectives but is particularly relevant for MPAn. Conservation objectives for which connectivity is important include biodiversity conservation and sustainability, population persistence, resilience, and fisheries management. Applying an ecosystem-based management approach is particularly important for species that use different ecosystems throughout their life cycle. Many studies promoted connectivity as a means for achieving demographic persistence through MPAs and MPAn (Margules and Pressey, 2000; Sala et al., 2002; Botsford et al., 2009; Bode et al., 2016), particularly in the face of climate change (Magris et al., 2014).

Current levels of area, number, and protection level of MPAs may be insufficient to ensure connectivity. Priority sites for future MPA designation should be informed by data on individual passive and active dispersal that ensure connectivity and should attempt to improve persistence of populations or species that are protected by MPAs. In certain cases, additional MPAs will need to be placed in areas recognized as being important for protecting genetic diversity, maintaining health of spawning stocks and creating stepping stones between existing MPAs (Pujolar et al., 2013; Crochelet et al., 2016; Zeng et al., 2017). Additionally, some existing MPAn may not be optimally sited initially for promoting or ensuring significant ecological connections among populations (Froukh and Kochzius, 2007; Guizien et al., 2012; Feng et al., 2016; Engelhard et al., 2017). Therefore, changes to current MPAn such as re-zoning, relocating or protecting adjacent habitats, have been proposed to improve connectivity (Bors et al., 2012; Guizien et al., 2012; Nakajima et al., 2017).

Here, we provide four recommendations on the incorporation of connectivity in the design of MPA(n).

### 5.1. Determine whether to prioritize connectivity as an ecological criterion

Connectivity should always be *considered* in the design of a MPA or MPAn but may not always be *implemented* due to logistical and data constraints or because its relative contribution to the effectiveness of the design may be low relative to other ecological or socio-economic criteria. Therefore, the first step is determining *whether* connectivity should be incorporated as a conservation feature. For certain habitats, species and metapopulation structures, connectivity should be prioritized. For example, landscape connections and fragmented habitats may depend on connectivity to maintain persistence by immigration to locally extinct or declining patches. Puckett and Eggleston (2016) found that a network of no-harvest oyster reserves in North Carolina was not self-persistent due to limited local retention and inter-reserve connectivity. Ensuring connectivity of threatened species with a mobile life history stage, whether larval, juvenile, or adult, is imperative for recovery, persistence of ontogenetic migrations, ecosystem connections, and fisheries. Populations exhibiting population genetic structure through subpopulations or dispersal barriers also benefit from connectivity considerations. For example, understanding subpopulation connections can allow for the prioritization of local connectivity of genetically similar populations. Froukh and Kochzius (2007) suggested that for the Fourline wrasse (*Larabicus quadrilineatus*) in the Gulf of Aqaba, the northern and southern subpopulations should be managed as two separate stocks.

There are also cases where the consideration of connectivity may be less important but depends on the conservation objective. In most cases, a feature that is only found in a single area or population would not need to be connected to adjacent areas. For example, the objective of the Basin Head MPA in New Brunswick, Canada, is to protect the asexual reproductive form of Irish moss, only found in that one area, that relies on the byssal threads of mussels as a substrate for attachment (DFO, 2011). Therefore, the protection of this species depends on the maintenance of mussel beds of *Mytilus edulis* in the area, which has different dispersal and reproductive characteristics. Connectivity should be actively minimized to avoid the spread of invasive species and pollutants, but there are multiple ways of meeting this objective. In a port with a large number of invasive species or area with high agricultural runoff, one approach might be to isolate these areas, by placing MPAs far away. Alternatively, protecting healthy ecosystems nearby is a different strategy and may combat negative connectivity vectors (e.g. by outcompeting invasive species).

Alongside other important aspects of design, such as size, habitat quality, and level of protection, connectivity can increase effectiveness of MPAs. Magris et al. (2018) analyzed data from 288 Mediterranean fish species with different ranges and suggested that species, particularly those with small ranges, benefited from the integration of representation and connectivity (Magris et al., 2018). When comparing connectivity and habitat quality, Berglund et al. (2012) argued that connectivity should be prioritized over habitat extent and quality; this suggestion is directly contradicted by Cabral et al. (2016), who argued that siting MPAs using connectivity metrics (source, sink, centrality) rarely produced optimal results over coupling habitat extent and quality, and suggested that habitat characteristics should be prioritized in spatial planning. However, it is not necessarily beneficial to prioritize these two ecological measures relative to one another because both are required to ensure

metapopulation persistence. It is important to note that connectivity considerations should not replace the use of other ecological indicators, but rather complement them (Magris et al., 2018).

The importance of incorporating connectivity in MPA design highlights the need for tools that can be used by managers to evaluate the role of connectivity in marine spatial planning. White et al. (2014) suggested an independent assessment to deduce the improvement gained by incorporating scientific knowledge on connectivity patterns into MPA design, and new tools becoming accessible to managers may prove useful. The R toolbox 'best MPA' aims to explore alternative MPA network designs and assess trade-offs of different ecological decisions (Daigle et al., 2015). The widely used spatial planning tool Marxan also allows for connectivity to be incorporated as a discrete feature or by replacing the boundary length modifier with connectivity values. Connectivity data can also be imported into Zonation, another spatial planning tool, to optimize for connections through corridors or apply penalties based on boundary lengths (Di Minin et al., 2014). A newly developed tool, MarxanConnect, provides a graphical user interface to incorporate connectivity matrices and landscape connectivity data into Marxan (<http://marxanconnect.ca/>). Simpler tools, such as a decision tree, can allow managers to incorporate size and spacing into MPAn planning, if data on connectivity are limited (Burt et al., 2014; D'Aloia et al., 2017; Smith and Metaxas, 2018) (See section 7.1.3 for more information on applying connectivity data into MPA design using spatial planning tools).

While there is clear evidence to support that connectivity in some cases improves the efficiency of designing MPAn (Magris et al., 2018), we acknowledge the current challenges and setbacks that may prevent its inclusion such as: data unavailability, competing social and economic goals, and time and funding constraints. Nonetheless, assuming connectivity objectives are met incidentally by inflating representation targets should only be considered as a last resort. Spatial planning tools are widely utilized, and their algorithms are designed to meet area-based targets; therefore, these tools do not select for well-connected areas, even when the 'clumping' factor is increased. Including landscape metrics of least cost path or Euclidean distance, which do not require any additional ecological data, can provide useful information about the proximity of populations to one another.

### 5.2. Identify the role of a MPA in supporting connectivity

When incorporating connectivity into the design of MPAn, it is essential to identify the role that each MPA plays in supporting connectivity. For example, the existence of source and self-replenishing populations enhance connectivity and persistence of a MPAn, whereas other MPAs in a network may serve as stepping stones or corridors that connect widely distributed species. In post-hoc connectivity evaluations of existing networks, MPAs containing these source populations, self-replenishing populations and central populations are often considered essential to the network (Christie et al., 2010; Berumen et al., 2012; Pusack et al., 2014; Gomes et al., 2016; Jahnke et al., 2017; Magris et al., 2018).

Transport of individuals across dispersal barriers can be facilitated by centrally located MPAs, increasing the efficacy of the latter (e.g. Ross et al., 2017). However, centrality is not always the best connectivity metric to optimize. Burgess et al. (2014) proposed that optimizing for local retention and therefore persistence is generally more advantageous. For example, the network of Mediterranean MPAs is not fully connected for the dusky grouper (*E. marginatus*), but single MPAs with high betweenness centrality values may be important for connectivity of the entire system (Andreollo et al., 2013). Therefore, considering centrality measures is important for identifying connectivity hotspots, but other metrics are better suited for decisions on the scale of the network.

Incorporating connectivity need not only provide benefits to the network, but also to surrounding unprotected areas, for example in fisheries, through export and overall population maintenance and growth. A passive drifter experiment at Riley's Hump in the Tortugas Ecological Reserve South indicated that the MPA may be a source of recruits for mutton snapper to the Florida Keys and southeast Florida and, therefore, may be acting as a fisheries reserve (Domeier, 2004). Export to surrounding areas depends greatly on the location and size of a single MPA. *E. marginatus*, *Pagellus erythrinus* and *Scorpaena porcus* benefit from the protection of the Medes Island MPA, which encompasses a known spawning area for these species (López-Sanz et al., 2011).

### 5.3. Identify appropriate spatial and temporal scales

If connectivity is to be implemented in the design of a MPAn, management units should be scaled based on realistic connectivity patterns. For example, white seabream (*Diplodus sargus*) and dusky grouper (*E. marginatus*) have two separate subpopulations in the area surrounding Sicily, concordant with oceanographic currents, suggesting that management units should represent these geographic differences (González-Wangüemert et al., 2012; Buchholz-Sørensen and Vella, 2016). In the western North Pacific, two genetic clusters of the neon damselfish (*Pomacentrus coelestis*) with minimal gene flow between them have been identified, possibly requiring separate MPAn for their management (Liu et al., 2011).

Dispersal is a key factor in determining the spatial scale of the management unit and varies among target species. Species with short dispersal distances and low representation in networks may be more vulnerable to stressors, whereas species with long-range dispersal, such as grey reef sharks, may require larger protection areas, and still spend substantial periods in unprotected areas (Gallego et al., 2017; White et al., 2017). On the west coast of North America, the brown rockfish, which exhibits high dispersal potential, was found to have low realized dispersal based on genetic divergence. It was recommended that a regional, rather than coast-wide scale be considered for MPAn design and that MPAs should be distributed with close

spacing across the entire species range as a buffer against environmental variability and fragmentation (Buonaccorsi et al., 2005).

The relevant spatial scale for management should be determined on a case-by-case basis, depending on the potential and, if known, realized dispersal of focal species on ecologically relevant scales (10s – 1000 s km). Miyake et al. (2011) suggested measuring dispersal from each larval source to adequately understand the variance in dispersal potential and suggested that in coastal systems a scale of 80 km is necessary to capture larval dispersal. In Central America, genetic analyses identified connectivity for spiny lobster at spatial scales beyond international boundaries; recruitment to the Mesoamerican Barrier Reef likely occurs from source populations outside national boundaries (Truelove et al., 2015). Considering spatial scales that encapsulate multiple habitats and ecosystems is essential for protecting species that move between habitats (Weeks, 2017).

Patterns of connectivity may also vary over time, highlighting the need for measurements at local spatial scales over multi-year time scales. For example, connectivity of reef fish between nodes in a MPAN varied by species and over time in Kimbe Bay, Papua New Guinea (Berumen et al., 2012). In California, the Garibaldi damselfish (*Hypsypops rubicundus*) exhibited a source-sink metapopulation on a bi-weekly time scale, but the pattern was not maintained at interannual time scales (Cook et al., 2014). Therefore, managers should caution against applying conservation strategies based on connectivity measures from a single point in time as they may not capture the full variation in dispersal patterns (Berumen et al., 2012; Pusack et al., 2014; Soria et al., 2014).

#### 5.4. Improve regional knowledge of patterns of connectivity

Increasing the taxonomic and geographic resolution of patterns in connectivity is needed for both scientific and management applications. For example, understanding the dispersal patterns of the white sea bream using otolith chemistry in Mediterranean rocky reefs led to a body of work on the connectivity of this important coastal species (Di Franco et al., 2012). This knowledge, in combination with connectivity patterns from other fish species, can be used to determine optimal size and spacing constraints to maintain connectivity in a MPAN. In Fijian reefs, large differences in population connectivity among species highlighted the need for management with more than a single unit (Drew and Barber, 2012). Coupled biophysical models have been used to quantify larval dispersal and determine potential population connectivity in shallow and coastal waters (Guizien et al., 2012; Trembl et al., 2012), but this approach is not feasible in the deep sea. Hilário et al. (2015) compiled data on pelagic larval duration as an indicator for dispersal distance for 93 species at 2 depth classes (eurybathic and deep) and proposed using a larval duration of 69 days to ensure a minimum dispersal for 75% of measured species (Hilário et al., 2015). Such metrics use the best available knowledge to inform connectivity for a broad group of taxa and can be updated as more information becomes available.

## 6. Challenges and limitations of this review

The level of documentation in the management literature limited our analysis of ecological criteria. A management plan includes selection criteria deemed important for a MPA, typically developed during a consultation process. If connectivity had not been included in a management plan, we were unable to distinguish whether this was because it had not been deemed a priority or was not considered at all. Not including connectivity could be because of lack of data, limited understanding of the process, or limited resources (perhaps supported by a value of information analysis).

For practical reasons, we restricted the scope of our study to regions with advanced systematic conservation planning, likely inflating the percentage of MPAs that consider connectivity. If we had included all MPAs worldwide, this percentage would most likely be much lower. There were also ample examples in the scientific literature where connectivity for a particular MPAN was evaluated, even when connectivity was not included as an original design element.

In the design of many MPAs, there were insufficient data to make inferences about connectivity. Assessments of meta-population connectivity over large spatial scales are essential to both establishing new MPAs and evaluating existing ones, but this information is lacking for most species (Fenberg et al., 2012). Our understanding of connectivity continues to expand, and significant advancements have been made since the 2000s. We have progressed from the need for a better understanding of the spatial and temporal scale of connectivity (Kritzer and Sale, 2004) to measuring connectivity for different taxa over broad areas and time scales (Cook et al., 2014). As the field continues to progress, frameworks should be optimized to introduce new information at each step in the MPA design process and in post-hoc evaluations of existing designs.

## 7. Future approaches for prioritizing connectivity

### 7.1. Framework for including connectivity in MPA design

As new MPAs and MPAN are designated, evaluating their efficacy and determining whether they achieve conservation objectives is essential. We have identified large regional differences in the planning process and consideration of connectivity. We have also identified a distinct difference in the class of connectivity data (landscape, demographic or genetic) used by scientists and managers. The accessibility of connectivity data and the language in which it is communicated to managers by scientists poses a source of disconnect between these two sectors. Therefore, future planning processes should attempt to rectify these differences and target regional improvements based on current progress, data availability and resources. For

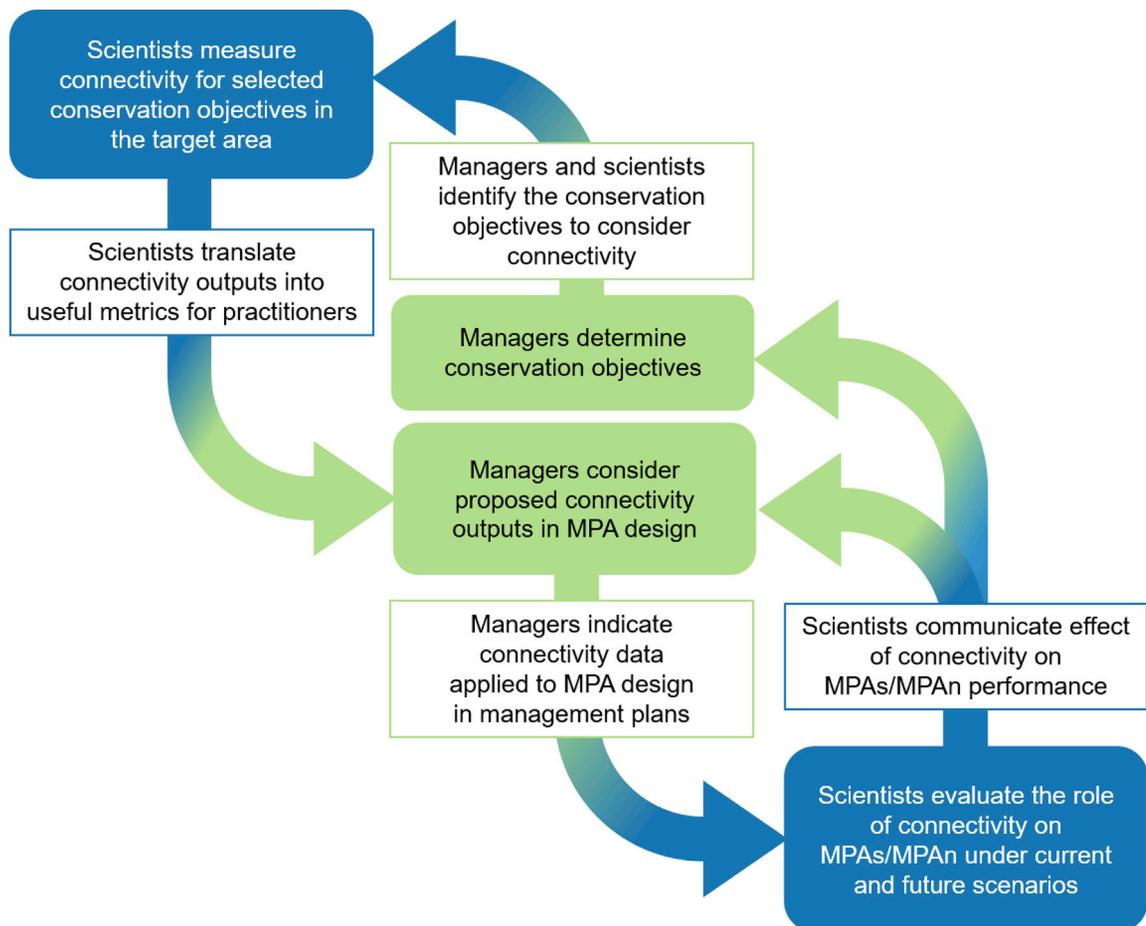
example, the GBR has advanced MPAn design strategies and tools available for adaptive management. In contrast, Canada and many other countries with lower data availability, may be limited to less sophisticated tools, such as decision trees (e.g. [Smith and Metaxas, 2018](#)). Matching the appropriate tool with data availability for regional assessments, as well as improving the accessibility of data and tools to managers, can help bridge the identified gap between science and management. Here, we propose a framework to implement connectivity during the planning phase and when evaluating the connectivity of existing MPAs and MPAn that attempts to bridge this gap ([Fig. 9](#)). Our framework clearly identifies the information that needs to be communicated and the roles of the two players at each stage. There is no distinct entry point to the proposed framework, but in most cases, it will naturally begin with the development of conservation objectives for a MPA/MPAn.

#### 7.1.1. Determine MPA/MPAn conservation objectives

For scientists to provide meaningful metrics of connectivity, managers must first identify conservation objectives ([Fig. 9](#)); these are typically representation-based, ranging from the protection of habitats (e.g. biogenic, unique, pristine) to species (e.g. spawning, foraging, nursery grounds), and are informed by data on, but not limited to, the 14 ecological criteria discussed above. Managers and scientists should then collaborate to identify which conservation objectives should consider connectivity and be guided by the 4 recommendations discussed above to incorporate connectivity into the design of MPAs (section 5).

#### 7.1.2. Evaluate and measure connectivity in the target area

Once the relevant conservation objectives and target areas have been identified, scientists can focus data collection that will allow them to calculate relevant metrics of connectivity ([Fig. 9](#)). For example, if the objective is to protect a source population, then considerations of larval output, dispersal and home range will be useful in determining the appropriate size



**Fig. 9.** Framework outlining steps in the design and evaluation of marine protected areas (MPAs) and networks of MPAs (MPAn) where connectivity can be incorporated. Blue boxes indicate steps where scientific research and advice are pertinent and green boxes indicate steps which rely on action by practitioners. Arrows indicate the facilitation of useable information between science and management sectors. See section 7.1 for a detailed description of the framework. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

and spacing of planned MPAs. Alternatively, if the objective is to provide stepping stones among MPAs, then network theory centrality metrics are one approach to derive meaningful metrics of connectivity.

Scientists will collect a suite of measurements of biological (ecological and genetic), physical, and geological variables. Habitat and species distributions (whether empirical measurements or suitable distribution modelling) can form the baseline to discern connections among populations and within the landscape. In turn, these data can be acquired from surveys, allowing for the calculation of landscape metrics (e.g. Euclidean distance or least cost path). In most cases, more specific data on the life history of species (e.g. pelagic duration, spawning time, larval behaviour) or more accurate location data allows for the calculation of more complex metrics. For example, tagging or taking tissue samples of individuals from multiple populations allows for the calculation of metrics such as home range, larval origin, or genetic analyses, respectively. With the addition of ocean circulation data (at relevant spatial scales) and physical models, flow, migration and probability connectivity matrices can be generated, and a suite of network theory metrics calculated (e.g. centrality, local retention).

### 7.1.3. Interpretation and consideration of connectivity outputs in MPA design

Accurate interpretation of connectivity data is key to implementation and requires close collaboration between scientists and managers (Fig. 9). Scientists are responsible for interpreting connectivity data and translating connectivity outputs into useful metrics for practitioners. For example, dispersal distances provide information about the spatial scale of movement at a particular life stage (most commonly propagule dispersal) and can therefore inform size and spacing of MPAs. Managers can either make MPAs large enough to incorporate self-recruitment or space MPAs near enough to ensure dispersal between adjacent MPAs. Another common form of connectivity output data is a connectivity matrix. In a connectivity matrix ( $p_{ij}$ ), columns are origins, rows are destinations and the entries represent the proportion of individuals in population  $i$  that originated in population  $j$  (Burgess et al. 2014; Cowen et al., 2007). Scientists can guide managers on how to use matrices in MPA design by communicating which metrics are useful for a particular conservation question. For example, if the objective of a MPA is to provide a hub or stepping stone that facilitates movement across an entire network, then a scientist could recommend the use of betweenness centrality. Populations that have a high betweenness centrality value have the highest number of shortest paths in a network (i.e. are centrally located). Once scientists outline how to apply connectivity data to MPAs design, managers can use this information to optimize MPA/MPAn design using decision support tools.

There is a wide range of decision support tools available to managers, including decision trees (Smith and Metaxas, 2018), integrative frameworks (Magris et al., 2014; D'Aloia et al., 2017) and spatial planning tools (Watts et al., 2008; Ardron et al., 2010; Di Minin et al., 2014; Daigle et al., 2018; Hanson et al., 2019) that can optimize protected area design. When some approaches are not feasible because of data (un)availability, or analytical and computational costs, frameworks and decision trees can be used to incorporate practical connectivity metrics into MPA design. Magris et al. (2014) suggested a framework for developing quantitative objectives to integrate connectivity through conservation objectives based on data requirements and the complexity of analysis. To consider species with ontogenetic movements, a framework developed by D'Aloia et al. (2017), that considers larval, juvenile and adult movement guides managers to determine where connectivity considerations are most important (e.g. adults with seasonal migrations), and which metrics and tools to use. In addition, Smith and Metaxas (2018) developed a decision tree for incorporating size and spacing guidelines into MPAn design based on larval dispersal, and juvenile and adult movement.

In cases where spatial or landscape data are available, a variety of decision support tools are available for managers for optimization of the arrangement of MPAs with multiple conservation objectives. Marxan is a reserve selection tool that balances cost with representation targets (Ardron et al., 2010), Marxan with Zones is a Marxan extension that allows users to incorporate different zones or protection levels into spatial planning (Watts et al., 2008), and Zonae Cogito is Marxan add-on used for data management and GIS visualization (Watts et al., 2011). Connectivity can be incorporated into Marxan as a conservation feature, or by using a connectivity matrix as a cost layer and tuning the boundary length modifier. MarxanConnect, a new software program, is another useful tool that derives connectivity metrics and translates them into quantitative conservation features or connectivity strength values (Daigle et al., 2018). Zonation, another reserve selection tool, balances biodiversity features, costs, and threats. It also has the capability to import connectivity data and apply boundary length penalties, and matrix or corridor connectivity (Di Minin et al., 2014). Prioritizr is a R package designed to create and solve conservation problems as mathematical optimization problems and can be used with a variety of exact algorithm solvers (e.g. heuristics or simulated annealing). Connectivity can be incorporated into prioritizr using penalties or constraints (Hanson et al., 2019) and using outputs from MarxanConnect. Once spatial planning tools have generated reserve solutions, and economic and social criteria are considered, practitioners are responsible for indicating within management plans (i) whether connectivity was considered in MPA design, (ii) included and (iii) the reasons for the decision, and (iv) the connectivity metrics used where relevant. This can allow scientists to evaluate the contribution of including (or not) connectivity in the performance and efficacy of MPAs and MPAn post-hoc.

### 7.1.4. Evaluate the connectivity of MPAs and MPAn

Connectivity of MPAs and MPAn must be evaluated by scientists to determine their efficacy, particularly in a rapidly changing climate and when MPAs are designated incrementally (Magris et al., 2018; Kininmonth et al., 2011, Fig. 9). Assessing the connectivity of a designated network uses many of the same approaches used to inform the design of MPAs. To evaluate whether a MPA is meeting conservation objectives related to connectivity, scientists should consider the four

recommendations outlined in section 5. To address high level conservation objectives at the network scale, additional approaches, such as population viability analysis or metapopulation growth rate can be used to evaluate persistence.

Where post-hoc evaluations of MPA effectiveness reveal that patterns of regional connectivity should be protected to meet conservation objectives, steps should be taken to improve management of these areas. Scientists are responsible for communicating the effect of connectivity on MPA/MPAn performance and making recommendations for future MPAs (Fig. 9). Recommendations may include adding new MPAs or adjusting boundaries or zoning of existing MPAs. Managers need to evaluate this new information and decide whether to implement it; however, adjusting existing MPAs is challenging, particularly legislatively. Even when scientific case studies have identified areas where changes to current MPAs should be applied, we did not find examples where scientific recommendations were used by practitioners.

The result of post-hoc evaluations of connectivity by scientists may also lead to the generation of new conservation objectives (e.g. protect ontogenetic migration of commercially important species in a target area over time). In this case, the steps of the framework should be followed again from the beginning.

### 7.2. Adaptive management: benefits of continuous feedback

Our framework identifies the steps and actors involved in the communication of information that is needed in the consideration of integrating connectivity in the design and management of MPAs and MPAn. The current gap between science and practice, in terms of connectivity, mirrors a similar challenge in the 1990s when managers were unaware of the tools for biodiversity conservation (e.g. reserve selection algorithms, gap analysis) available in the scientific literature (Prendergast et al., 1999). As available tools become more accessible to practitioners, it is presumed that connectivity will be incorporated into planning processes and post-hoc evaluations more frequently.

The Aichi biodiversity targets require immediate action from many countries and candidate areas for MPAs need to be identified and designated under the current level of information on all ecological criteria including connectivity. This underscores the importance of quantifying connectivity in newly designated networks after 2020. The proposed framework facilitates the feedback between managers and scientists to improve the application of connectivity data at local scales.

### 7.3. Future challenges

Integrating our understanding of connectivity over various spatial scales for a wide range of species with different ecological characteristics is a major challenge for conservation science (Magris et al., 2018), and will only be further complicated in a changing ocean that is threatening the functionality of current MPAs (Lagabriele et al., 2014; Magris et al., 2014; Bruno et al., 2018). Networks of MPAs, when well-designed and with high levels of protection, can reduce biodiversity loss and safeguard important ecological processes to promote recovery (Roberts et al., 2018). In tropical and low-latitude areas, sea-surface temperature and oxygen concentration will exceed natural variability in 42% of 309 existing marine reserves, reducing the benefits of these MPAs to mitigate threats to marine biodiversity (Bruno et al., 2018). Species ranges, ecosystem functioning, reproduction, and spawning windows will likely change due to warming temperatures and increased concentrations of CO<sub>2</sub>, and larvae, juveniles and adults will experience different and new environments (Chen et al., 2011; Pankhurst and Munday, 2011; Nagelkerken and Connell, 2015). These changes may affect connectivity patterns and will require adaptive management, and more explicit recommendations based on empirical studies by scientists, and actions by managers. As scientific information on connectivity develops, it should be made easily available to managers to ensure it can be applied rapidly and effectively.

Ensuring effective and well-connected MPAn will continue after 2020, as the current target of 10% will likely not meet the goals of MPAs intended by the CBD (Gaines et al., 2010; O'Leary et al., 2016) with a new target of >30% having been proposed (IUCN, 2014). Considering both representation and connectivity is likely the best conservation strategy for protecting the persistence of biodiversity (Magris et al., 2018).

Our review demonstrates that the current use of connectivity in MPA design is minimal and geographically biased. However, connectivity has been increasingly considered in MPA planning and should continue to do so with the development of useful tools. We suggest a framework that will promote the implementation of connectivity into the design of MPAs and help bridge the gap between scientific understanding and application by practitioners.

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.gecco.2019.e00569>.

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