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Multi-species genetic objectives in spatial conservation planning

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Abstract:	The increasing threats to biodiversity and global alteration of habitats and species distributions make it increasingly necessary to consider evolutionary patterns in conservation decision-making. Yet there is no clear-cut guidance on how genetic features can be incorporated into conservation planning processes, with multiple molecular markers and several genetic variation measures for each marker type to choose from. Genetic patterns also differ between species, but the potential trade-offs amongst genetic objectives for multiple species in conservation planning are currently understudied. This study compares spatial conservation prioritizations derived from two metrics of both genetic diversity (nucleotide and haplotype diversity) and genetic isolation (private haplotypes and local genetic differentiation) for five marine species. The findings show that conservation plans based solely on habitat representation noticeably differ from those additionally including genetic data, with habitat-based conservation plans selecting fewer conservation priority areas. Furthermore, all four genetic metrics selected approximately similar conservation priority areas, which is likely a result of prioritizing genetic patterns across a genetically diverse array of species. Largely, the results suggest that multi-species genetic conservation objectives are vital to create protected area networks that appropriately preserve community-level evolutionary patterns.

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Abstract

The increasing threats to biodiversity and global alteration of habitats and species distributions make it increasingly necessary to consider evolutionary patterns in conservation decision-making. Yet there is no clear-cut guidance on how genetic features can be incorporated into conservation planning processes, with multiple molecular markers and several genetic variation measures for each marker type to choose from. Genetic patterns also differ between species, but the potential trade-offs amongst genetic objectives for multiple species in conservation planning are currently understudied. This study compares spatial conservation prioritizations derived from two metrics of both genetic diversity (nucleotide and haplotype diversity) and genetic isolation (private haplotypes and local genetic differentiation) for five marine species. The findings show that conservation plans based solely on habitat representation noticeably differ from those additionally including genetic data, with habitat-based conservation plans selecting fewer conservation priority areas. Furthermore, all four genetic metrics selected approximately similar conservation priority areas, which is likely a result of prioritizing genetic patterns across a genetically diverse array of species. Largely, the results suggest that multi-species genetic conservation objectives are vital to create protected area networks that appropriately preserve community-level evolutionary patterns.

Keywords: genetic diversity, genetic isolation, Marxan, conservation genetics, spatial prioritization, inter-tidal ecology

Introduction

Anthropogenic pressures such as overfishing, movement of alien species, habitat alteration and human mediated climate impacts are major drivers of change in marine ecosystems (Halpern et al. 2008; Mead et al. 2013). In order to combat further degradation of marine and coastal environments and to provide resilience for the future, marine protected areas (MPAs) have been shown to be an effective management tool (Edgar et al. 2014). However, limited resources and high socio-economic dependencies of local communities on marine ecosystem services requires a balance of marine conservation objectives and the associated costs of conservation actions (Bottrill et al. 2008). To accommodate trade-offs in conservation planning, quantitative approaches are often implemented and are highly effective at identifying locations best suited for conservation action (Wilson et al. 2009).

Evidence-based decision processes usually involve setting objectives to conserve specific amounts of spatially explicit biodiversity features such as habitat type, species richness, or migration patterns (Margules & Pressey 2000; Leslie 2005), and then reaching these objectives in the most cost-efficient manner (Naidoo et al. 2006). However, while biodiversity features such as habitat type or species distributions are important to include in conservation plans, and have informed the vast majority of spatial plans to date, they fail to represent evolutionary patterns such as phylogenetic diversity (Mouillot et al. 2016), population structure (von der Heyden 2009) and local adaptation (McMahon et al. 2014). Because standing genetic variation can play a major role in providing resilience to future change (Ehlers et al. 2008), it is essential that conservation objectives incorporate genetic patterns both within and between species (Pressey et al. 2007; Sgrò et al. 2010). Some efforts have been made to integrate genetic metrics from single species (Sork et al. 2009; Beger et al. 2014), and surrogates for genetic patterns across multiple species (Carvalho et al. 2010) into conservation planning, yet the integration of multiple genetic metrics from multi-species data sets is currently lacking within conservation planning theory.

Much empirical work has been done on spatially delineating populations and conservation units using genetic information (Moritz 2002; Funk et al. 2014). However, the actual implementation of genetic data into conservation planning remains an exception and not the rule (von der Heyden 2009; Laikre 2010), particularly in marine systems (Beger et al. 2014; von der Heyden et al. 2014). Ambiguity in the interpretation of genetic data and a need for a framework to guide its use hinder the integration of genetic metrics into spatial planning (Waples et al. 2008; Shafer et al. 2014). For example, objectives need to be clear and measurable, define relevant spatial and temporal scales, and address environmental and socio-economic uncertainty (Mace & Purvis 2008; Kool et al. 2015). Nonetheless, there are examples of genetic metrics within conservation objectives, such as delineating stocks for fisheries management and assessing gene flow (von der Heyden et al. 2014) and advancements have been made on formulating objectives for genetic metrics in conservation planning (see Beger et al. 2014). The next step towards operational conservation planning for evolutionary processes requires integrating planning objectives for various genetic metrics across multiple species as conservation features.

This paper aims to firstly compare conservation scenarios using four genetic metrics for five phylogenetically and functionally different species occurring in a marine climate change hotspot. Secondly, this work aims to disentangle the conservation priorities that may occur when including multiple genetic metrics from species with dissimilar genetic patterns. Broadly this study asks the following questions: 1) do priorities differ for genetic-based conservation plans, compared to a baseline using only habitat-based objectives?; 2) do priorities differ between conservation plans based on different genetic diversity and isolation metrics?; 3) what is the effect of averaging genetic metrics from multiple species rather than incorporating them individually?; and finally 4) do multiple species and genetic metrics contribute equally to the combined conservation outcome? Answers to these questions are a prerequisite to formulating a generalizable framework for conserving multi-species genetic patterns.

Methods

This study focuses on the west coast of South Africa (bounded by 18.3’E, -34.1’S and 16.8’E, -29.3’S). We included genetic data from five obligate rocky shore species that share similar distributions along the South African coastline. All species were collected from the same seven sites along the South African west coast (Fig. 1), one of South Africa’s most threatened marine environments (Sink et al. 2011).

The five species for which we included genetic data are the granular limpet (*Scutellastra granularis*), super klipfish (*Clinus superciliosus*), Cape urchin (*Parechinus angulosus*), tiger topshell winkel (*Oxystele tigrina*) and cushion star (*Parvulastra exigua*). These species were chosen due to their different life history characteristics, reproductive strategies and functional roles within the rocky shore community (Table 1 Supporting Information; Mertens 2012). Several studies suggest that these five species exhibit complex evolutionary histories along the west coast of South Africa (von der Heyden et al. 2011; Muller et al. 2012; Wright et al. 2015). Based on mitochondrial DNA (mtDNA) datasets, the five study species display variable genetic structure, different migration rates and a wide range of genetic diversity values (Tables 1 & 2 Supporting Information; Mertens 2012). Therefore, we expect them to represent the genetic spectrum of species within the regional rocky shore community.

Genetic metrics

Genetic metrics were derived from mtDNA regions, specifically a fragment of the cytochrome oxidase I (COI) gene for the invertebrates and a section of the mtDNA control region for the klipfish (*C. superciliosus* – Table 1 Supporting Information). The evolutionary mechanisms of mtDNA are well understood from a comparative phylogeographic and evolutionary perspective (Bowen et al. 2014), making mtDNA regions useful markers for integrative genetic conservation planning efforts. Our analyses included four genetic metrics, namely haplotype diversity (*h*), nucleotide diversity (π) (*sensu* Nei 1987), number of private haplotypes, and local genetic differentiation (Table 1). Each of these is highly relevant to conservation as they capture historical and contemporary processes shaping extant patterns of biodiversity (discussed in more detail below).

Conservation relevance of chosen genetic metrics

Genetic diversity is recognized as being an important conservation feature as high levels of genetic diversity and variation in genotypes/haplotypes can increase individual fitness and population resilience (Hughes et al. 2008) and is the raw material for natural selection to act on (Lande & Shannon 1996). Further, there is evidence that genetic diversity may correlate with species richness (Messmer et al. 2012; Wright et al. 2015; Selkoe et al. 2016), and potentially enhance ecosystem function and resilience (Reusch et al. 2005; Bernhardt & Leslie 2012). Conversely, low genetic diversity makes a population more susceptible to inbreeding depression and possible extinction (Charlesworth & Charlesworth 1987).

Additionally, meta-population persistence and individual population resilience can be inferred by comparing the genetic distinctiveness of populations (Mortiz 2002; Beger et al. 2014). If a population is genetically isolated, it may be less resilient (Van Oppen & Gates 2006; Vollmer & Palumbi 2007) and should be delineated as an individual management unit (Palumbi 2003). Therefore, such populations have conservation importance simply because they are different, making them analogous to a rare species. Further, unique genotypes/haplotypes or rare haplotype frequencies may be a result of natural selection, which in the absence of markers that measure adaptive variation could indicate local adaptation if ecological or environmental factors are driving genetic patterns. On the contrary, low distinctiveness and uniqueness is also of conservation value because populations that are not in isolation are genetically and demographically connected, making them potentially more resistant and resilient to change. Lastly, the middle classes of each genetic metric was given a lower, yet moderate target as a precautionary conservation approach, as those areas may turn into low or high ranking sites in the future.

Data generation and implementation

We used TCS (Clement 2000) to collapse all genetic datasets into haplotypes and Arlequin v3.5 (Excoffier et al. 2010) to calculate π and *h.* Local genetic differentiation was calculated in Arlequin, with a sequential AMOVA including two populations; one being the site of interest, and the other being all sites combined. Unique haplotypes were counted and labeled as private haplotypes for each population. We then interpolated the genetic data from the seven point localities using an inverse distance weighting technique in ArcGIS v10.2 (ESRI 2014). We recognize that this procedure represents a simplified version of natural genetic patterns, and that genetic point data should rather be predicted using environmental parameters, yet there is currently no framework on how to model genetic patterns in marine environments (Beger et al. 2014).

For each genetic metric (haplotype diversity (*h*), nucleotide diversity (π), number of private haplotypes, and local genetic differentiation), we created three classes (low, medium, high) using equal intervals across their measured range of values and set conservation targets for each class. However, to set appropriate targets for each genetic metric, it is important to first identify conservation objectives (Carwardine et al. 2009). Here, our conservation objective was to represent regional genetic variability to include evolutionary significant areas into a marine reserve network. We followed a similar protocol to Beger et al. (2014) and set the target to represent 50% of the high and low classes, and 30% of the medium class, as each class may have different evolutionary value.

Spatial prioritizations incorporating genetic metrics were carried out for each of the five species individually, as well as a sixth scenario including values averaged across all five species for each of the seven sampling locations. Averaging the values for each genetic metric summarizes the interspecific genetic composition within the planning region, and may identify important areas for conserving ecosystem function (Whitham et al. 2006; Hersch-Green et al. 2011). This 'community genetics' approach may be more effective with large data sets (such as in Wares et al. 2002; Selkoe et al. 2016), but its applicability to spatial management has yet to be explored.

Conservation prioritization analyses

Conservation priority areas were identified with Marxan, a decision support tool that uses an algorithm to minimize the reserve system cost of the entire network, whilst meeting a set of biodiversity targets (Ball et al. 2009).

Our planning domain included near-shore intertidal areas along the ~800km length of the west coast of South Africa (Fig 1A), extending 500m seaward to 500m inland. The baseline conservation features are five rocky shore habitat types identified in the 2011 National Biodiversity Assessment (Sink et al. 2011); namely exposed, sheltered, mixed, boulder and hard ground rocky shores. After performing a sensitivity analysis, we chose a conservation target to include 40% of each habitat. To represent lost exploitation opportunities, we included cost data from Majiedt et al. (2013), which quantifies a diverse array of socio-economic pressures currently identified along the South African west coast. The habitat and cost features remained constant across all planning scenarios and are termed 'baseline' for the remainder of this study.

In order to explore the effect of each genetic metric, as well as each of the five species on conservation priorities, we compared trade-offs between variables using the following: 1) A genetic metric approach where each metric was included separately for all species (change in genetic metric); 2) A species approach where all genetic metrics were included for each species separately (change in species); 3) A combined approach where each species combined with each genetic metric was treated separately (termed ALL); and 4) An averaged approach where genetic metrics were averaged across the five species resulting in one spatial dataset per genetic metric (termed AVG; Table 2). The conservation targets of 50% and 30% remained the same for each genetic feature across the scenarios.

Additionally, to examine the effect of different conservation objectives, we chose a single metric, local genetic differentiation, and solely protected either high or low ranking areas. For the objective of conserving genetically distinct areas, we set the target to protect 60% of high-ranking areas, and zero percent of the medium and low ranking areas. For the counter objective of conserving genetically connected sites we set the target to conserve 60% of low ranking areas and zero percent of the medium and high ranking areas.

For each of the scenarios, we ran Marxan 100 times to account for variability across solutions, and maintained calibration parameters constant. We then followed the protocols in Harris et al. (2014) to analyze similarities between scenarios, performing non-metric multi-dimensional scaling (nMDS) ordination based on Jaccard resemblance matrices in R 3.2.2 (R Development Core Team 2012).

Finally, to quantify the similarity between scenarios we calculated Pearson correlation coefficients (from selection frequency values for each planning unit) between each pair of scenarios. To obtain the average amount of congruence between scenarios with either a change in species or genetic metric, we then took the average of the Pearson correlation coefficients for each of the two scenario groupings. To further quantify the trade-offs associated with either a change in species or genetic metric, we calculated the range in number of selected planning units, as well as Marxan cost and score from both scenarios with a change in species or genetic metric.

Results

Conservation priority maps

High-priority sites for conservation differ between the baseline scenario and each genetic scenario (Fig. 1, B-H), yet all scenarios highlight areas along the entire coastline as priority sites. There are minor differences between the genetic scenarios, with each one identifying multiple clusters of conservation priority areas, roughly extending from those chosen in the baseline scenario (Fig. 1, E-H). The haplotype diversity scenario has the most definitive high priority clusters (Fig. 1, E), followed by the local genetic differentiation scenario (Fig.1, G). Both the private haplotypes and nucleotide diversity scenarios show smaller conservation priority clusters that are more spread out along the coastline (Fig. 1, F,H). Lastly, the planning units chosen throughout all genetic scenarios (Scenarios 2-5) indicate that the northern region, as well as select areas throughout the mid-and southern west coast are conservation genetic 'hotspots' (Fig. 2).

Dissimilarity plots

The baseline scenario forms a distinct cluster and is highly dissimilar from the genetic scenarios (Fig. 2A). Solutions from each genetic scenario form a distinct cluster, with little overlap between scenarios (Fig. 2B). The scenarios including nucleotide diversity and number of private haplotypes for all species are the most similar, followed by those including haplotype diversity and local genetic differentiation. The ALL scenario shows a broad range of solutions, of relatively equal similarity to each of the scenarios including one genetic metric. Lastly, the scenario with the averaged genetic metrics is most dissimilar to all of the other genetic scenarios and there is no congruence between the two scenarios that include all genetic metrics (ALL and AVG).

The nMDS plot based on the dissimilarities between single species and multi-species genetic scenarios (Fig. 2C) shows little concordance between the solutions, with each species highlighting different conservation priority areas. Most single-species scenarios form tight clusters with highly similar solutions, with the exception of the granular limpet (*S. granularis*), which shows a broad range of spatial solutions. The two scenarios including all species (ALL and AVG) show no congruence, with the AVG scenario displaying the most divergent set of solutions.

Quantifying conservation trade-offs

The Pearson correlation coefficients mirror the nMDS plots (Table 3, Supporting Information) and show that no one solution is highly dissimilar to the others with the exception of the baseline scenario. The average similarity between scenarios with a change in genetic metric is just slightly lower than the scenarios with a change in species (Table 2). However, the ranges in number of selected planning units, Marxan cost and score are larger across the scenarios with a change in species versus a change in genetic metric (Table 2).

Discussion

Intraspecific genetic variation is the foundation of biological diversity, and thus conserving the adaptive potential of organisms is pivotal to their long-term persistence. Despite calls to inform conservation decisions with genetic and genomic information (Funk et al. 2014; Shafer et al. 2014), few examples exist where evolutionary patterns have been translated into actionable conservation objectives (Laikre 2010) with existing studies focusing solely on single species (Sork et al. 2009;

Beger et al. 2014; von der Heyden et al. 2014). Importantly, our findings demonstrate that no single species can adequately represent multi-species genetic patterns because spatial conservation priority sites vary between different species. Further, within the context of understanding habitat-only versus genetic scenarios, each scenario including a genetic metric highlights noticeably more priority areas compared to the baseline scenario. This indicates that not accounting for community genetic metrics in conservation plans will underrepresent genetic patterns in MPA networks, thereby jeopardising the protection of the processes driving spatial patterns of biodiversity (Klein et al. 2009).

Conservation planning with and without genetic data

We found a clear separation between conservation priority areas derived from the baseline scenario and the genetic scenarios, confirming similar results for data from a single species (Beger et al. 2014). While conservation priority areas from each genetic metric seem to roughly correlate to those in the baseline scenario, the priority sites chosen throughout all genetic scenarios (Fig. 2, D) are not representative of the baseline, meaning that genetic 'hotspots' are not spatially associated with the different habitat types. Using multi-species conservation objectives, we show that dissimilarities between habitat-based and genetics-based conservation plans result in widely different scenarios, further supporting the need to include genetic information into conservation planning (von der Heyden 2009). In the context of a rapidly changing climate, this finding has important implications for the persistence of species and communities, as failing to protect standing genetic variation increases the likelihood of losing genetic variants which may be more resilient to change (Barrett & Schulter 2008).

Conservation trade-offs between genetic measures

All genetic scenarios choose approximately similar areas as conservation priorities, with slight discrepancies in conservation selection patterns (Fig. 1, E-H). This suggests that protecting a percentage of high, medium and low ranking areas for a single genetic metric from multiple species, will most likely also capture priority sites arising from other genetic metrics. The broadly similar conservation priorities between the different genetic metrics are unexpected, as different evolutionary and demographic processes and statistical approaches relate to the different metrics (Table 1). The similarities between the conservation priority areas from the separate genetic metrics could be a result of the broad spectrum of genetic patterns within our five study species. For instance, when different conservation objectives (conserving only high or low ranking areas) are compared from just a single metric (local genetic differentiation), we find that some sites are chosen as conservation priority areas for both objectives (Fig. 3). This illustrates that while the genetic metrics may have different spatial patterns, these differences can be captured in the conservation solutions in some instances without spatial rearrangement of priorities.

Whilst the different genetic metrics broadly select similar conservation priority areas along the coastline, there are discrepancies between the different genetic scenarios. For instance, the scenarios including nucleotide diversity and private haplotypes leads to smaller, but more widely spread, areas of conservation priority when compared to those based on haplotype diversity and local genetic differentiation (Fig. 1, E-H). The similar conservation priorities between nucleotide diversity and private haplotypes, and haplotype diversity and local genetic differentiation are unexpected, as it would be likely that the two scenarios including either a diversity (*h*

/ π) or isolation (private haplotypes / local genetic differentiation) metric would be more similar to each other. However, the similar conservation spatial patterns between nucleotide diversity and private haplotypes in our study are most likely because there is little agreement in the genetic values between species, which leads to the more widely spread selection of planning units.

Conservation trade-offs across different species

Each of the five study species shows highly variable conservation solutions (which is expected since each species is characterized by unique genetic characteristics), with little congruence between scenarios representing different species (Fig. 2B). Larval dispersal is recognized as an important driver of these differences (White et al. 2010), but the interaction between pelagic larval duration and population structure varies hugely between species (Selkoe & Toonen 2011). Furthermore, interspecific genetic differences can be due to forces unrelated to dispersal, such as habitat availability and time since re-colonization (Selkoe et al. 2014; Selkoe et al. 2016). Therefore the inclusion of genetic information from multiple species, even if they have similar biological characteristics (e.g. distribution ranges, life history) is critical, as even functionally similar species can be characterized by very different evolutionary histories and contemporary genetic patterns (Wright et al. 2015). Moreover, the results show little congruence between phylogeographic patterns and conservation spatial patterns, as the two most highly structured species (*P. angulosus* and *P. exigua*) and the two panmitic species (*S. granularis* and *O. tigrina*) do not have spatial solutions that are more similar to each other than those species with different phylogeogpraphic patterns (Fig. 2C; Table 2 Supporting Information). In addition, the number of selected planning units also does not correspond with phylogeographic patterns, as the two species with the most planning units chosen are *P. angulosus* and *S. granularis*, which have the highest and lowest genetic structure respectively (Table 2; Table 2 Supporting Information). This suggests that if the objective is to identify genetically diverse or unique areas, then solely including phylogeographic patterns may not capture the full extent of genetic relationships between sites.

Our findings also show distinct conservation priorities occur with the inclusion of either single-species or multi-species genetic metrics (Fig. 2B). While the inclusion of multi-species objectives is recommended in conservation planning (von der Heyden 2009; Toonen et al 2011; Magris et al. 2015), no previous studies have explored how conservation objectives aimed at protecting community-level genetic composition compare with those aimed at single species as indicators for overall genetic variability. We show that including genetic information for multiple species independently (ALL scenario) gives conservation priorities that are equally similar to the priorities derived from genetic data from each individual species (Fig. 2, C; Table 3 Supporting Information). Thus, we recommend including multiple species as features individually instead of using the multi-species average as a single conservation feature in conservation planning (Fig. 2, A-C). However, averaging genetic metrics may be a viable approach with larger or more homogeneous data sets. For example, Selkoe et al. (2016) found that within a 47 species genetic dataset, many species showed compatible genetic patterns, which lends some support for averaging genetic measures. Further, the effects of averaging genetic datasets with missing data has yet to be explored, as well as the potential trade-offs of having multiple species with averaged values versus having fewer species with non-averaged values.

Conservation trade-offs across genetic metrics and species

We found that the average similarity between spatial priorities is only slightly larger with a change in species versus change in genetic metric. This implies that the inclusion of either an additional genetic metric or species will alter the conservation priorities to a similar degree. However, the results also show that the scenarios with a change in species lead to a greater range in number of planning units chosen, as well as Marxan cost and score, which means a change in species is more likely to result in conservation solutions with a broader range in priority areas chosen in the 'optimum' spatial plan. Overall, the results suggest that a change in species leads to an overall greater change in number of planning units selected (which in turn leads to greater trade-offs in cost and score), yet the areas where the planning units are selected will spatially be more similar to each other with a change in species than genetic metric.

Concluding remarks

This study shows that, using mtDNA as a marker, conservation plans can be developed to preserve not only habitat features, but also the evolutionary aspects of species distributions. Given that a majority of studies dealing with population genetic structure to date have used mtDNA as one of the markers (Bowen et al. 2014; Keyse et al. 2014), there is ample opportunity for exploring the approaches laid out here with different species and geographical areas. For example, there are a large number of single and multi-species genetic data sets available for the Indo-Pacific (see Horne et al. 2008; Gaither et al. 2010; Keyse et al. 2014) and the Mediterranean (see Carlsson et al. 2004; Duran et al. 2004; Carreras et al. 2007), which could be utilized and included into management plans. A key hurdle is the mismatch in scales between genetic variability and planning areas; but genetic data is well suited to inform regional-scale and multi-lateral conservation efforts. Although several additional aspects, such as comparing conservation priority areas derived from both neutral and adaptive markers, and including both local and pairwise genetic measures from multiple markers have not yet been explored, our work provides a baseline for investigating these conservation scenarios. In addition, with the development of landscape genetics and genotype-by-environment tests, it should become possible to derive environmental or ecological factors driving genetic patterns in natural systems. This information may help predict future changes in genetic variation and allow us to account for such changes within conservation planning frameworks.

Supporting Information

Life history traits (Appendix S1) and genetic variation indices (Appendix S2) for the five study species are available online, along with quantitative trade-offs between scenarios (Appendix S3). The authors are solely responsible for the content and functionality of these materials.Queries (other than absence of the material) should be directed to the corresponding author.

Literature Cited

Ball IR, Possingham HP, Watts M. 2009. Marxan and relatives: software for spatial conservation prioritisation. Spatial conservation prioritisation: quantitative methods and computational tools. Pages 185-195. Oxford University Press, Oxford.

Barrett RD, Schluter D. Adaptation from standing genetic variation. 2008. Trends in Ecology & Evolution **23:**38-44.

Beger M, Selkoe KA, Treml E, Barber PH, von der Heyden S, Crandall ED, Toonen RJ, Riginos C. 2014. Evolving coral reef conservation with genetic information. Bulletin of Marine Science **90:**159-185.

Bernhardt JR, Leslie HM, 2013. Resilience to climate change in coastal marine ecosystems. Marine Science **5.**

Bottrill MC, et al. 2008. Is conservation triage just smart decision making? Trends in Ecology & Evolution **23:**649-654.

Bowen BW, et al. 2014. Phylogeography unplugged: comparative surveys in the genomic era. Bulletin of Marine Science **90:**13-46.

Carlsson J, McDowell JA, Diaz-James, PÍ, Carlsson JE, Boles SB, Gold JR, Graves JE. 2004. Microsatellite and mitochondrial DNA analyses of Atlantic bluefin tuna (*Thunnus thynnus thynnus*) population structure in the Mediterranean Sea. Molecular Ecology **13:**3345-56.

Carreras C, et al. 2007. The genetic structure of the loggerhead sea turtle (*Caretta caretta*) in the Mediterranean as revealed by nuclear and mitochondrial DNA and its conservation implications. Conservation Genetics **8:**761-75.

Carwardine J, Klein CJ, Wilson KA, Pressey RL, Possingham HP. 2009. Hitting the target and missing the point: target-based conservation planning in context. Conservation Letters **2:**4-11.

Charlesworth D, Charlesworth B. 1987. Inbreeding depression and its evolutionary consequences. Annual Review of Ecology and Systematics pp. 237-268.

Clement M, Posada DCKA, Crandall, KA. 2000. TCS: a computer program to estimate gene genealogies. Molecular Ecology **9:**1657-1659.

Duran S, Pascual M, Turon X. 2004. Low levels of genetic variation in mtDNA sequences over the western Mediterranean and Atlantic range of the sponge *Crambe crambe* (Poecilosclerida). Marine Biology **144:**31-5.

Edgar GJ, et al. 2014. Global conservation outcomes depend on marine protected areas with five key features. Nature **506:**216-20.

Ehlers A, Worm B, Reusch TB. 2008 Importance of genetic diversity in eelgrass *Zostera marina* for its resilience to global warming. Marine Ecology Progress Series **355:**1-7.

Environmental Systems Research Institute (ESRI), 2014. ArcGIS Desktop 10.2 Geostatistical Analyst.

Excoffier L, Lischer HE. 2010. Arlequin suite ver 3.5: a new series of programs to perform population genetics analyses under Linux and Windows. Molecular Ecology resources **10:**564-567.

Funk WC, McKay JK, Hohenlohe PA, Allendorf FW. 2012. Harnessing genomics for delineating conservation units. Trends in Ecology & Evolution **27:**489–96.

Gaither MR, Toonen RJ, Robertson DR, Planes S, Bowen BW. 2010. Genetic evaluation of marine biogeographical barriers: perspectives from two widespread

Indo-Pacific snappers (*Lutjanus kasmira* and *Lutjanus fulvus*). Journal of Biogeography **37:**133-47.

Halpern BS, Walbridge S, Selkoe KA, Kappel CV, Micheli F, D'Agrosa C, Bruno JF, Casey KS, Ebert C, Fox HE, Fujita R. 2008. A global map of human impact on marine ecosystems. Science **319:**948-952.

Harris LR, Watts ME, Nel R, Schoeman DS, Possingham HP. 2014. Using multivariate statistics to explore trade-offs among spatial planning scenarios. Journal of Applied Ecology **51:**1504-14.

Hersch-Green EI, Turley NE, Johnson, MT. 2011. Community genetics: what have we accomplished and where should we be going? Philosophical Transactions of the Royal Society of London B: Biological Sciences **366:**1453-1460.

Horne JB, van Herwerden L, Choat JH, Robertson DR. 2008. High population connectivity across the Indo-Pacific: congruent lack of phylogeographic structure in three reef fish congeners. Molecular Phylogenetics and Evolution **49:**629-38.

Keyse J, Crandall ED, Toonen RJ, Meyer CP, Treml EA, Riginos C. 2014. The scope of published population genetic data for Indo-Pacific marine fauna and future research opportunities in the region. Bulletin of Marine Science **90:**47-78.

Klein C, Wilson K, Watts M, Stein J, Berr, S, Carwardine J, Smith MS, Mackey B, Possingham H. 2009. Incorporating ecological and evolutionary processes into continental-scale conservation planning. Ecological Applications **19:** 206-217.

Kool J, Appleyard S, Bax N, Ford J, Hillman K, Howe S, Jackson EL, Kirkman H, Parr A, Slawinski D, Stafford-Bell R. 2015. Lessons learned at the interface of marine ecology and environmental management in Australia. Bulletin of Marine Science **91:**469-476.

Laikre L. 2010. Genetic diversity is overlooked in international conservation policy implementation. Conservation Genetics **11:**349–354.

Lande R & Shannon S. 1996. The role of genetic variation in adaptation and population persistence in a changing environment. Evolution **50:** 434-437.

Leslie HM. 2005. A synthesis of marine conservation planning approaches. Conservation Biology **19:**1701-1713.

Mace GM, Purvis A. 2008. Evolutionary biology and practical conservation: bridging a widening gap. Molecular Ecology **17:**9-19.

Magris RA, Treml EA, Pressey RL, Weeks R. 2015. Integrating multiple species connectivity and habitat quality into conservation planning for coral reefs. Ecography DOI: 10.1111 /ecog.01507.

Majiedt P, Holnes S, Sink K, Oosthuizen A, Chadwick P. 2013. Systematic Marine Biodiversity Plan for the West Coast of South Africa. Unpublished report. Pages 46.

South Africa National Biodiversity Institute, Cape Town.

Margules CR, Pressey RL. 2000. Systematic conservation planning. Nature **405:**243-253.

McMahon BJ, Teeling EC, Höglund J. 2014. How and why should we implement genomics into conservation? Evolutionary Applications **7:**999-1007

Mead A, et al. 2013. Human-mediated drivers of change—impacts on coastal ecosystems and marine biota of South Africa. African Journal of Marine Science **35:**403-25.

Mertens, LEA, 2012. Using gene flow and phylogeography of multiple marine species to plan a Marine Protected Area network for the West Coast of South Africa. Master thesis. Stellenbosch University, South Africa.

Moritz C. 2002. Strategies to protect biological diversity and the evolutionary processes that sustain it. Systematic biology **51:**238-254.

Mouillot D, et al. 2016. Global marine protected areas do not secure the evolutionary history of tropical corals and fishes. Nature Communications **7**.

Muller CM, von der Heyden S, Bowie RC, Matthee CA. 2012. Oceanic circulation, local upwelling and palaeoclimatic changes linked to the phylogeography of the Cape sea urchin *Parechinus angulosus*. Marine Ecology Progress Series **468:**203.

Naidoo R, Balmford A, Ferraro PJ, Polasky S, Ricketts TH, Rouget M. 2006. Integrating economic costs into conservation planning. Trends in Ecology & Evolution **21:**681-687.

Nei M. 1987. Molecular evolutionary genetics. Columbia University Press, New York, NY.

Palumbi SR. 2003. Population genetics, demographic connectivity, and the design of marine reserves. Ecological Applications **13:**146-158.

Pressey RL, Cabeza M, Watts ME, Cowling RM, Wilson KA. 2007. Conservation planning in a changing world. Trends in Ecology & Evolution **22:**583-592.

Reusch TB, Ehlers A, Hämmerli A, Worm B. 2005. Ecosystem recovery after climatic extremes enhanced by genotypic diversity. Proceedings of the National Academy of Sciences of the United States of America **102:**2826-2831.

Selkoe KA, Toonen RJ. 2011. Marine connectivity: a new look at pelagic larval duration and genetic metrics of dispersal. Marine Ecology Progress Series **436:**291-305.

Selkoe KA, Gaggiotti OE, Bowen BW, Toonen RJ. 2014. Emergent patterns of population genetic structure for a coral reef community. Molecular Ecology **12:**3064-3079.

Selkoe KA, Gaggiotti OE, Treml EA, Wren JL, Donovan MK, Toonen RJ. 2016. The DNA of coral reef biodiversity: predicting and protecting genetic diversity of reef assemblages. Proceedings of the Royal Society of London B: Biological Sciences **283.** DOI: 10.1098

Shafer ABA, et al. 2014 Genomics and the challenging translation into conservation practice. Trends in Ecology & Evolution **30:**78-87.

Sink K, et al. 2012. National Biodiversity Assessment 2011: Technical Report. Volume 4: Marine and Coastal Component. South African National Biodiversity Institute, Pretoria.

Sgrò CM, Lowe AJ, Hoffmann AA. 2011. Building evolutionary resilience for conserving biodiversity under climate change. Evolutionary Applications **4:**326–337.

Sork VL, Davis FW, Grivet D. 2009. Incorporating genetic information into conservation planning for California valley oak. In Proceedings of the 6th symposium on Oak Woodlands: California's Oaks: today's challenges, tomorrow's opportunities. Pages 497-509. Pacific Southwest Research Station, Forest Service, US Department of Agriculture, Albany.

Team, R., 2012. Development core. R: A language and environment for statistical computing. Vienna, Austria.

Toonen RJ, et al. 2011. Defining boundaries for ecosystem-based management: a multispecies case study of marine connectivity across the Hawaiian Archipelago. Journal of Marine Biology **2011:**13.

Van Oppen MJ, Gates RD. 2006. Conservation genetics and the resilience of reef-building corals. Molecular Ecology **15:**3863-3883.

Vollmer SV, Palumbi SR. 2007. Restricted gene flow in the Caribbean staghorn coral *Acropora cervicornis*: implications for the recovery of endangered reefs. Journal of Heredity **98:**40-50.

von der Heyden S, Bowie RC, Prochazka K, Bloomer P, Crane NL, Bernardi G. Phylogeographic patterns and cryptic speciation across oceanographic barriers in South African intertidal fishes. 2011. Journal of Evolutionary Biology **24:**2505-19.

von der Heyden S, Beger M, Toonen RJ, Juinio-meñez MA, Ravago-gotanco R, Fauvelot C, Bernardi G. 2014. The application of genetics to marine management and conservation: examples from the Indo-Pacific. Bulletin of Marine Science **90:**123–158.

Waples RS, Punt AE, Cope JM. 2008. Integrating genetic data into management of marine resources: how can we do it better? Fish and Fisheries **9:**423-449.

Wares JP. 2002. Community genetics in the Northwestern Atlantic intertidal. Molecular Ecology **11:**1131-1144.

Whitham TG, et al. 2006. A framework for community and ecosystem genetics: from genes to ecosystems. Nature Reviews Genetics **7:**510-523.

White C, Selkoe KA, Watson J, Siegel DA, Zacherl DC, Toonen RJ. 2010. Ocean currents help explain population genetic structure. Proceedings of the Royal Society of London B: Biological Sciences DOI:10.1098

Wilson KA, Cabeza M, Klein CJ. 2009. Fundamental concepts of spatial conservation prioritization. Pages 16-27. Spatial Conservation Prioritization: Quantitative Methods and Computational Tools. Oxford University Press New York.

Wright D, Bishop JM, Matthee CA, von der Heyden S. 2015. Genetic isolation by distance reveals restricted dispersal across a range of life histories: implications for biodiversity conservation planning across highly variable marine environments. Diversity and Distributions **21:**698-710.

Table 1- The four genetic features compared in this study, what they measure, and their relevance to conservation planning.

Genetic feature	Definition	Conservation relevance
Haplotype diversity (*h*)	- The probability that two randomly sampled individuals differ in their haplotypes (a.k.a. mitochondrial DNA allele types)	- As haplotype diversity represents frequency-weighted variation (Nei 1987), it incorporates gene flow, which may make it a more suitable metric to identify management units (Funk et al. 2014)
Nucleotide diversity (π)	- The average number of nucleotide differences per site between any two DNA sequences chosen randomly from the sample population	- Nucleotide diversity represents the absolute standing genetic variation, which may make it a more suitable metric to identify evolutionary significant units (Funk et al. 2014)
Number of private haplotypes	- Private haplotypes (or alleles) are unique to a single population -A measure of how unique a site is compared to other sites	- A site with a high number of private haplotypes might be genetically isolated, rendering it less resilient to stochastic, catastrophic features such as oil spills

		(Lande & Shannon 1996) - Genetically unique populations may be interpreted as evolutionary hotspots (Beger et al. 2014)
Local genetic differentiation	- A measure of how much a population's genetic diversity differs from the mean of all of the populations combined	- If a population is genetically isolated from the other populations then it may be less resilient - A population may also be genetically distinct due to local evolutionary processes, in this case the site can play an important role in the meta-population (Beger et al. 2014)

Table 2- Describes the various scenarios compared in Marxan.

Scenario No.	Conservation features included	Abbreviation
1	Habitat type (baseline)	B
2	Haplotype diversity	H
3	Nucleotide diversity	N
4	Local genetic differentiation	L
5	Private alleles	P
6	All genetic metrics for *C. superciliosus*	CS
7	All genetic metrics for *O. tigrina*	OT
8	All genetic metrics for *P. angulosus*	PA
9	All genetic metrics for *P. exigua*	PE
10	All genetic metrics for *S. granularis*	SG
11	All genetic metrics as five individual layers corresponding to each species	ALL
12	Each genetic metric as single layer averaged over the five species	AVG

Table 3- Measures of dissimilarity across scenarios altering either the species or genetic feature included as conservation features.

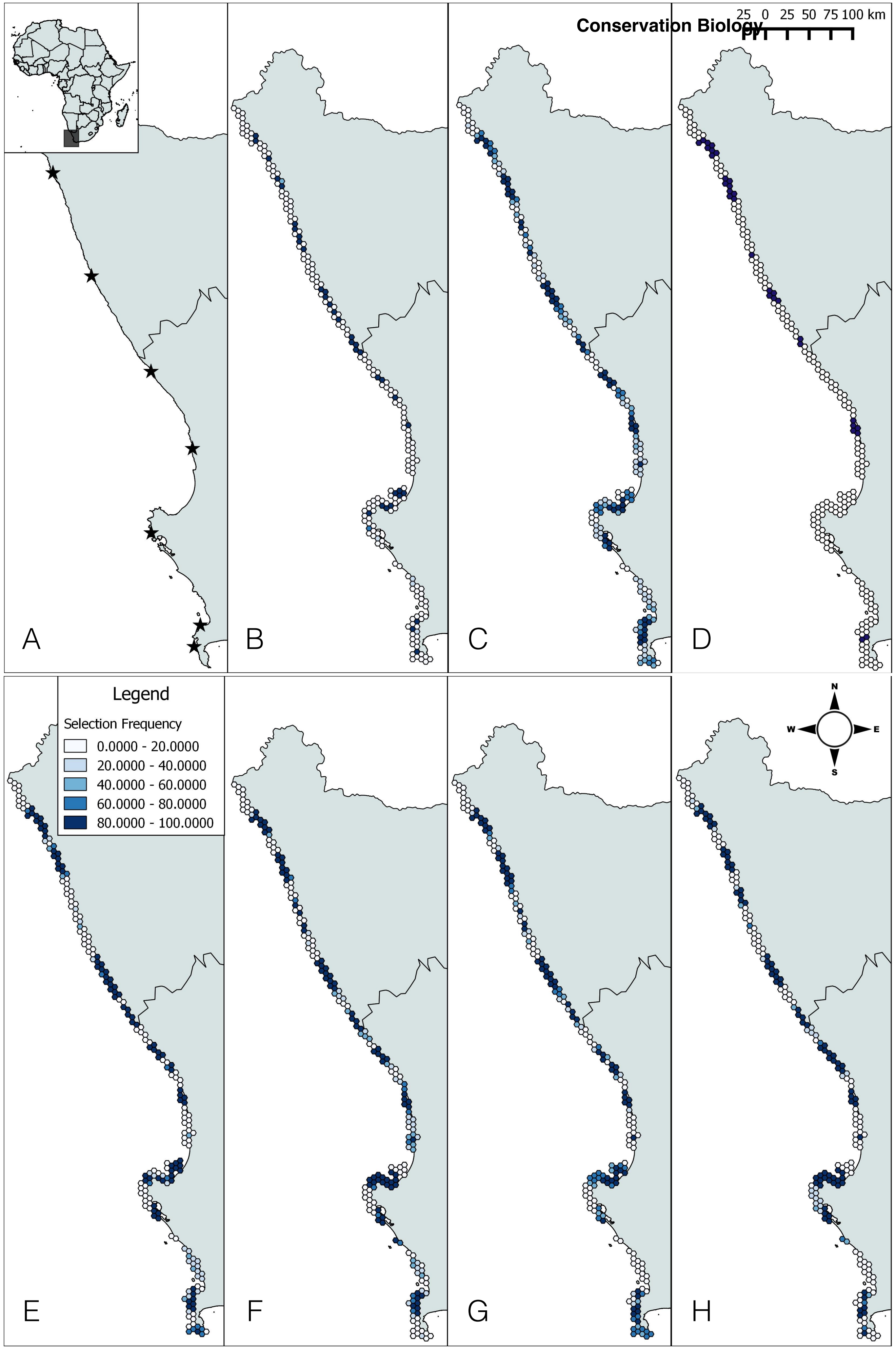
Measure of dissimilarity	Change in species	Change in genetic feature
Average Pearson correlation	0.61	0.56
Range in cost	95	50
Range in score	91	44
Range in planning units	7	5

Figure Legends

Fig. 1- The seven sampling locations (A) and conservation priorities from the Baseline (B), ALL (C), Haplotype diversity (E), Nucleotide diversity (F), Local genetic differentiation (G), and Private haplotype (H) scenarios, as well as planning units chosen by each genetic metric scenario (D). Conservation priority maps are based on selection frequencies; darker planning units have a higher selection frequency.

Fig. 2- Non-metric multi-dimensional scaling ordination plots illustrating the dissimilarities between the 100 solutions of the baseline and genetic scenarios (A), solely the genetic scenarios (B), as well as the single-species scenarios (C).

Fig. 3- The conservation spatial patterns derived from conserving 60% of either low genetic differentiation (A) or high differentiation (B). Areas highlighted in red are selected with both objectives.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A
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F
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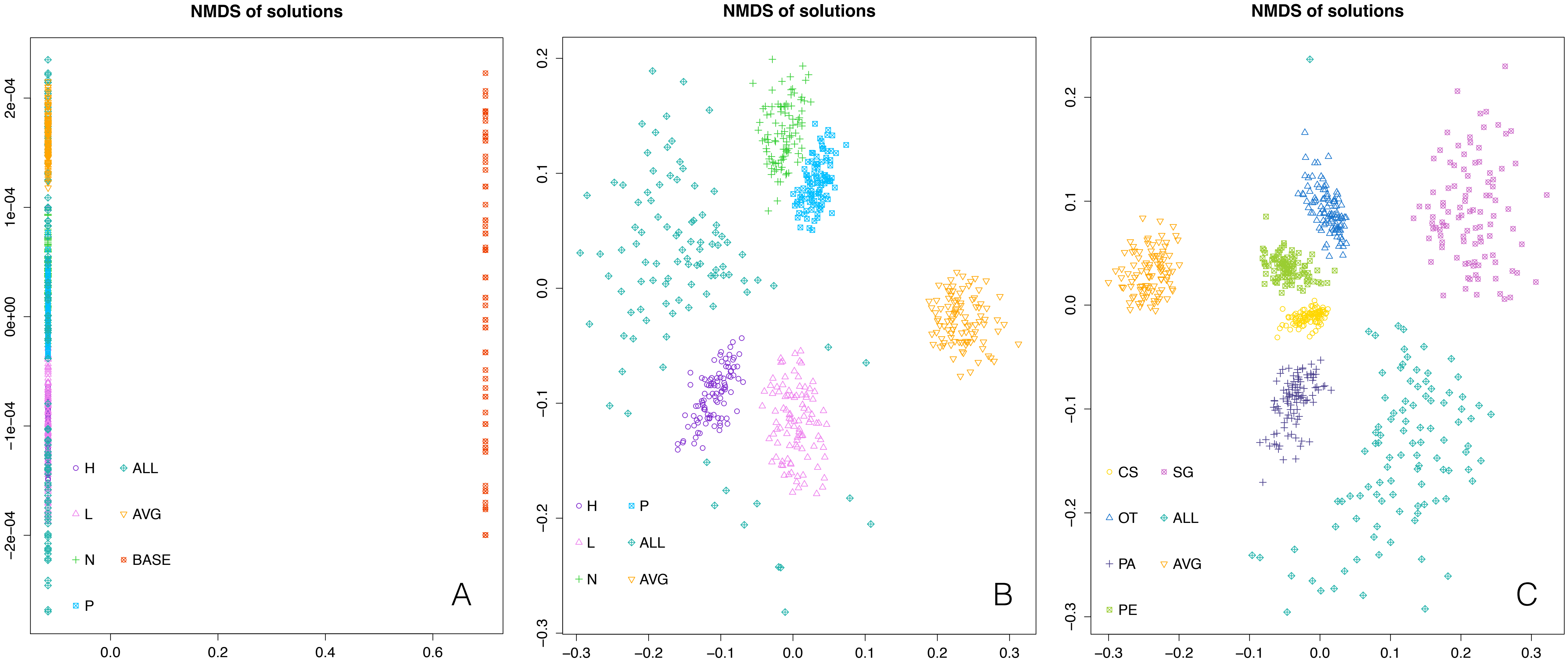
NMDS of solutions
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−2e−04
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N
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A
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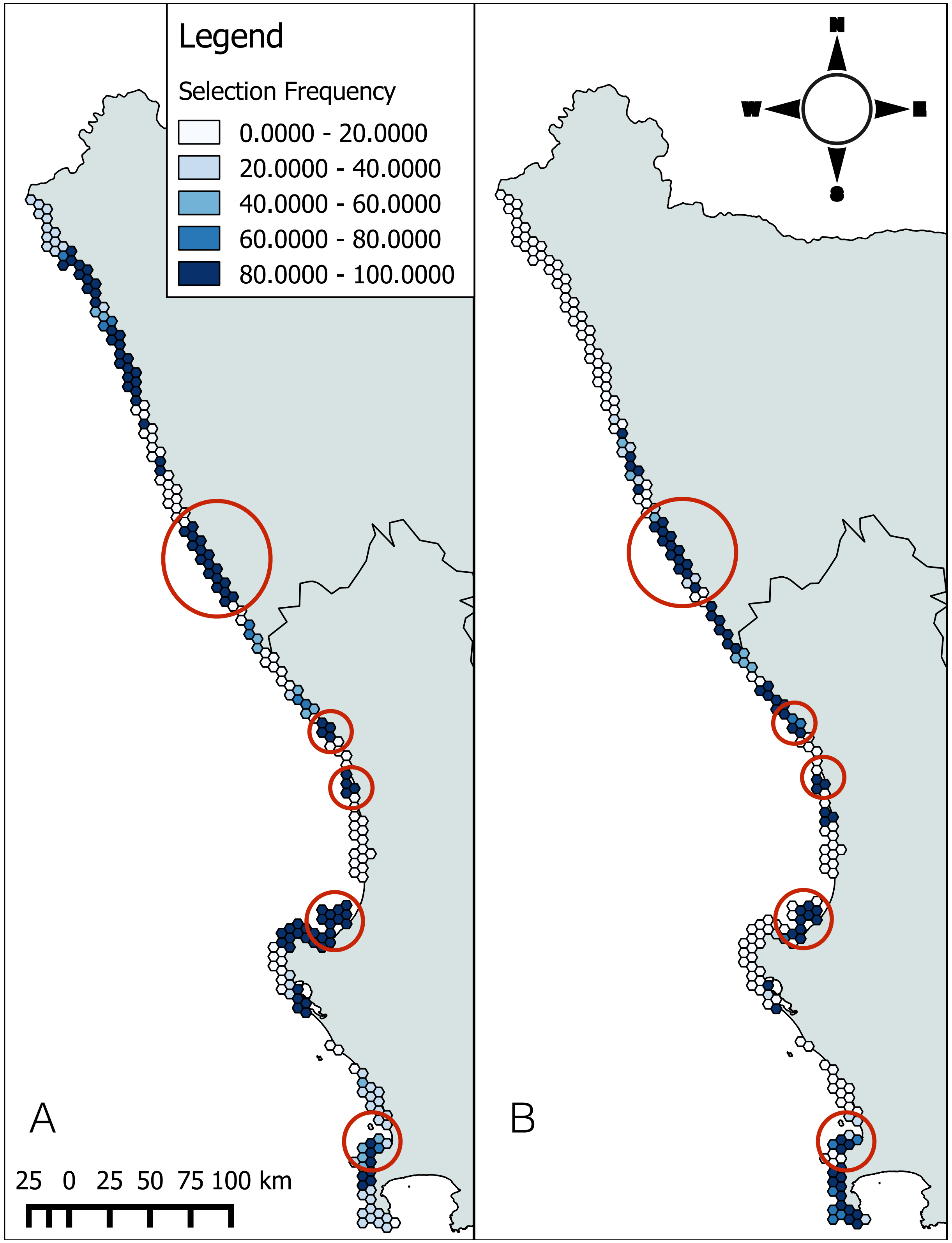
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