Geographic surrogates of genetic variation for selecting island populations for conservation

Running title: Geographic surrogates for genetic variation

Authors, affiliations and email (in contribution order):

1.-Rocío Ponce-Reyes (corresponding author)
Environmental Decisions Group, the School of Biological Sciences, University of Queensland, St Lucia QLD 4072, Australia
r.ponce@uq.edu.au
Ph. +61 7 3365 2494
Fax +61 7 3365 1655

2. - Sonya M. Clegg (s.clegg@griffith.edu.au)
- Environmental Futures Research Institute and Griffith School of Environment, Gold Coast Campus, Griffith University QLD 4222, Australia;
- Biodiversity and Geosciences Program, Queensland Museum, PO Box 3300, South Brisbane, QLD 4101, Australia; and
- Division of Biology, Imperial College London, Silwood Park, Ascot, Berkshire SL5 7PY, UK.

3. - Silvia B. Carvalho (silviacarvalho@cibio.up.pt)
- The School of Biological Sciences, University of Queensland, St Lucia QLD 4072, Australia; and
- CIBIO - Centro de Investigação em Biodiversida de e Recursos Genéticos da Universidad do Porto, R. Padre Armando Quintas, 4485-661 Vairão, Portugal;

4. - Eve McDonald-Madden (Eve.Mcdonald-Madden@csiro.au)
- The School of Biological Sciences, University of Queensland, St Lucia QLD 4072, Australia; and
- ARC Centre of Excellence for Environmental Decisions, University of Queensland, St Lucia QLD 4072, Australia
- Climate Adaptation Flagship, CSIRO Ecosystem Sciences 41 Boggo Rd, Dutton Park 4102 QLD Australia

5. - Hugh P. Possingham (h.possingham@uq.edu.au)
- The School of Biological Sciences, University of Queensland, St Lucia QLD 4072, Australia;
- Division of Life Sciences, Imperial College London, Silwood Park, Ascot, Berkeshire, UK; and
- ARC Centre of Excellence for Environmental Decisions, University of Queensland, St Lucia QLD 4072, Australia

Abstract

Aim

Threatened species often exist in small numbers in isolated populations. Limited financial resources usually constrain conservationists to allocate funds to a subset of these populations. Since obtaining information required to maximize the amount of genetic and phenotypic variation protected can be costly and time-consuming, the utility of surrogates should be explored. This study tests the efficacy of three simple and cost-effective geographic measures in capturing genetic and phenotypic variation of fragmented populations when setting conservation priorities.

Location

Vanuatu archipelago.

Methods

We used neutral genetic data (mtDNA and microsatellites) and morphometric data (a proxy for functional variation) for two bird species displaying different patterns of regional population genetic structure: *Zosterops flavifrons* and *Z. lateralis*. We tested the performance of three geographical surrogates (maximising: geographic distance between islands; area of islands; geographic representation of islands), in representing divergence between and diversity within populations, constrained to the number of islands being protected.

Results

Maximizing geographic separation of sites provided the best surrogate for a constrained budget (<50% of the populations) for both species. For a larger protected area system (>50% of the populations) the spatially most representative sites were often more effective. Selecting islands based on size retained about half of within population genetic diversity; however this was not much higher than selecting the islands randomly.

Main Conclusions

The ability of surrogates to capture genetic or phenotypic variation varied depending on the species, genetic markers and number of islands selected. While imperfect, selection of populations based on simple geographic surrogates for genetic and phenotypic variation will generally be better than random selection for conserving the evolutionary potential of

threatened populations when time and money limit a more thorough and direct analyses of genetic and phenotypic variation.

Keywords: conservation management, genetic distance, geographic distance, area, Vanuatu, *Zosterops*

Introduction

Despite rapid declines (Balvanera *et al.*, 2006), economic resources available to biodiversity conservation are limited (James *et al.*, 1999). Managers and policy makers need to choose strategies that maximize conservation of single species within financial constraints (McDonald-Madden *et al.*, 2008). A crucial decision faced by managers is how much time and money should be allocated to compile and sample data to identify the most appropriate populations in which to invest (Possingham, 2007; Grantham *et al.*, 2008; 2009).

Maximum representation and persistence of biodiversity achieved at a minimum cost, are the central goals of conservation plans (Moilanen *et al.*, 2009). The majority of conservation plans focus on representing biodiversity patterns rather than on persistence (Frankel, 1974; Smith *et al.*, 1993; Moritz, 2002). However, it is essential to include the processes affecting both the amount and distribution of biological variability and the ability for organisms to adapt and evolve (Crandall *et al.*, 2000; Mace & Purvis, 2008).

Divergence among populations accumulated through time may lead to speciation (Slatkin, 1987), and high genetic diversity within populations increases reproductive viability, resilience to catastrophes, diseases and changing conditions (Soulé, 1987). Thus, researchers have emphasized both the importance of maximizing protection of the most divergent populations (Vane-Wright *et al.*, 1991; Faith, 1992; Moritz, 1994; Crandall *et al.*, 2000; Moritz, 2002; Redding & Mooers, 2006; Bonin *et al.*, 2007; Isaac *et al.*, 2007) and for identifying and protecting within-population genetic diversity (Petit *et al.*, 1998; Vandergast *et al.*, 2008; Thomassen *et al.*, 2011). Ideally, knowledge of adaptive genetic variation levels would be used to assess these attributes. However, information from neutral loci is generally employed to measure the distribution of genetic variation, with ensuing inferences for past and future adaptive processes (Moritz, 1994).

Restricted funds for conservation and the urgency of some decisions, sometimes impede the process of gathering and analysing genetic information. More easily obtained information that provides a degree of surrogacy for conserving genetic variation across populations is an alternative when planning for evolutionary process protection. Effective biodiversity surrogates ensure adequate representation of other biodiversity features (Moritz, 1994; Crandall *et al.*, 2000; Sarkar *et al.*, 2005; Rodrigues & Brooks, 2007). Only few studies have attempted to determine the effectiveness of surrogates of genetic diversity in conservation

119 planning. While species richness is a generally effective surrogate of phylogenetic diversity
120 at the between species level (Rodrigues *et al*., 2011), effective intra-specific surrogates have
121 not yet been established.
122
123 Surrogates for intraspecific genetic variation of fragmented populations could be derived
124 from geographic distances between fragments and their area. The strong biogeographical
125 basis of these surrogates means they can be used anywhere in the world without detailed
126 environmental information. Isolation-by-distance (IBD) patterns can reflect the relationship
127 of genetic divergence between populations and geographic distance. IBD patterns, where
128 genetic and geographic distance between populations are positively correlated (Wright,
129 1943), are commonly reported in the population genetic literature (Peterson & Denno, 1998;
130 Crispo & Hendry, 2005; Jenkins *et al.*, 2010). However the strength of IBD relationships will
131 likely determine the surrogacy degree for genetic divergence i.e. towards genetic isolation
132 under zero gene flow conditions or towards genetic panmixia under unrestricted gene flow
133 conditions (Hutchison & Templeton, 1999).
134
135 Fragment area, as a surrogate for genetic diversity within populations can be used as a proxy
136 for population size, and population size and genetic diversity often show a positive
137 relationship (Frankham, 1996). In small populations, the effects of genetic drift are more
138 pronounced, rare alleles are lost via genetic drift, whereas larger populations maintain higher
139 levels of genetic diversity (Wright, 1931; Lande & Barrowclough, 1987).
140
141 A third potential surrogate derived from geographic data aims to capture adequate
142 representation (*sensu* Faith & Walker (1996)). This surrogate, based on so-called "locations
143 problems" finds the optimal location of an object in space by minimising the distance
144 between selected and unselected objects. For example, in choosing a certain number of
145 islands from an archipelago, the set of islands with the shortest average distance to all other
146 islands would be considered representative of the geographical space covered by the
147 archipelago. This representative spatial arrangement, might capture the largest range of
148 between-population divergence and within-population diversity of a widely distributed
149 species. Naturally formed fragments or islands are unlikely to be regularly spaced, therefore
150 the representative islands are most likely to be drawn from geographically separated clusters,
151 thereby maximising population divergence. These same representative islands might have a

greater opportunity for gene flow from the widest range of other island populations (regardless of their area), thereby maximising within-population diversity.

Naturally fragmented distributions in watersheds, ecoregions or bioregions have been applied as explicit surrogates for ecological and evolutionary processes incorporating environmental and/or habitat gradients and/or geographic barriers in the planning process (Cowling & Pressey, 2001; Klein *et al.*, 2009). Here, we focus on oceanic island populations, even though these surrogates could be used in other island-type landscapes, such as mountain tops or rainforest fragments. Island populations generally have high conservation value because isolated populations are often genetically and/or phenotypically distinct (Wilson *et al.*, 2009) but exist in relatively small populations with lower levels of genetic diversity than mainland populations (Whittaker & Fernández-Palacios, 2007). These features can increase their vulnerability to natural or anthropogenic disturbance (Rosenzweig, 1995).

According to the rationale outlined above, we aim to determine the effectiveness of: 1) maximising geographic distance between islands as a surrogate for between-population variation; 2) maximising geographic area as a surrogate for within-population variation; and 3) spatial representativeness as a surrogate for capturing between- and within-population variation. In each case, we considered both neutral variation (neutral molecular markers) and putatively adaptative variation (morphological measurements). We analysed variation in *Zosterops flavifrons* and *Z. lateralis,* bird species with coincident distributions across the Vanuatu archipelago (Fig. 1). The species' have different population genetic structures, providing an excellent opportunity to assess the general effectiveness of geographic surrogates for genetic variation for species and the amount of genetic variation captured under different conservation scenarios. Throughout, we use the term 'island' to refer to single-island populations of *Z. lateralis* or *Z. flavifrons*.

Methods

Study area

Vanuatu is a Y-shaped oceanic archipelago about 2,000 km east of Northern Australia (Fig. 1), which comprises 13 main islands (>160km^2) and nearly 100 smaller ones formed along three volcanic belts, beginning approximately 20–22 Myr ago, with the bulk of current land area formed ≤0.5 Myr (Mallick, 1975). The environmental conditions (climate, soil and

vegetation type) can be grouped into northern (and central) islands and southern islands (Hamilton *et al.*, 2010). The northern islands are wetter and less thermally variable but have more soil (Quantin, 1975) and vegetation types (ten out of the 12 major structural vegetation types recognised by Gillison (1975) occur only in northern and central islands). This pattern reflects the geological origin of the archipelago and is consistent across vertebrate and invertebrate fauna with congruent breaks in species assemblages (Hamilton *et al.*, 2010). In Vanuatu, eight of the 127 bird species recorded are listed as endangered or vulnerable (Dutson, 2011). Their declines are attributed to forest loss and degradation, introduced predators and to a lesser extent hunting (Dutson, 2011).

Z. flavifrons is endemic to the Vanuatu archipelago having colonized around 2-4 Myr ago, while *Z. lateralis* is not endemic and represents a more recent colonization, <0.5 Myr ago (Phillimore *et al.*, 2008; Black, 2010). Multiple morphological subspecies have been described for both species (Mees, 1969) most of which show limited congruence with phylogenetic information (Phillimore *et al.*, 2008; Black, 2010). Additionally, *Z. flavifrons* has been divided into two groups based on plumage colour, 'yellow' and 'dark' (Mayr 1945; Mees 1969; see Fig. 1). A comparison of regional genetic population structure between these species showed that distance-mediated gene flow influenced population structure in *Z. lateralis*, with highest connectivity among the central and northern islands of the archipelago (Clegg & Phillimore, 2010). In contrast, the population structure of *Z. flavifrons* showed a partial shift towards a drift-mediated system, with a higher level of population structure and weaker influence of distance-mediated gene flow (Clegg & Phillimore, 2010). Within island population genetic structure has not been investigated, however most of the islands are relatively small (being some tens of kilometres wide at their widest point) and within- island population genetic divergence is unlikely to be on par with between-island divergence. However finer-scale genetic structure may occur on the larger islands, such as Espiritu Santo and Malekula.

Assessing the neutral genetic value of island subsets

Neutral genetic variation of *Z. flavifrons* and *Z. lateralis* populations in the Vanuatu archipelago has previously been quantified using mitochondrial DNA (mtDNA; 351bp of ND3 and 308 bp of cytochrome b (Phillimore *et al.*, 2008; Black, 2010) and microsatellite genotypes: eight loci for *Z flavifrons* and 11 loci for *Z. lateralis* (Phillimore *et al.*, 2008; Clegg & Phillimore, 2010). To measure genetic divergence between populations, matrices of

pairwise genetic distances among island populations were calculated from mtDNA sequence and microsatellite genotypes (see Appendix 1 and Supplementary Online Material for details). Genetic diversity within populations was measured by microsatellite allelic richness. Since available morphological information could be used *a priori* in conservation decisions, we repeated the analysis of genetic data for each of the *Z. flavifrons* plumage colour groups considered separately (see Appendix 2, Supplementary Online Material).

Between-population divergence

All modelling described below was performed in the R framework for statistical computing (R Development Core Team, 2010). Genetic divergences among island populations were estimated with the Neighbour –Joining method in MEGA (Tamura *et al.*, 2007). We created a tree for each genetic divergence index (P-net distance and pairwise F_{ST} for *Z. flavifrons* and pairwise F_{ST} for *Z. lateralis*) (Suppl. Figs.S1-3, respectively). Then the genetic divergence was calculated by adding the branch lengths of each tree of all possible combinations of choosing *k* islands from the total number of islands, *n* (eq. 1). The number of possible combinations (C) is given by:

$$C_k^n = \frac{n!}{(n-k)!\,k!}\text{, where:} \qquad (1)$$

$n_{flavifrons}$=13; and $k_{flavifrons}$=2, 3,…, 13; or

$n_{lateralis}$=11; and $k_{lateralis}$= 2, 3,…, 11.

Genetic divergence (GV) for each combination of *k* islands for both species were ranked from the highest GV_k (maximum genetic divergence; MaxGV) to the lowest ranked GV_k (minimum genetic divergence; MinGV). To allow comparison between the different genetic indices (P-net or pairwise F_{ST}) we calculated the percentage that each genetic value of *k* represented in the total genetic divergence (MaxGV).

Within-population diversity

We used microsatellite allelic richness as a measure of within-population diversity. Allelic richness is standardized according to the population with the smallest sample size (Mousadik & Petit, 1996). To calculate allelic richness for sets of islands, we identified all possible

combinations of *k* islands as described previously, and collapsed the microsatellite genotypes for selected islands into a "new" population. For example, if $k_{flavifrons}$= 3 out of the set I={A,B,C,D,E,F,G,H,I,J,K,L,M}, one possible combination of *k* islands would be C_1= {A,B,C}. The number of alleles in C_1 were counted (such that shared alleles in A, B and C were counted only once) and the combined sample size calculated. We used the repeated random subsampling method (in the R package standArich v1.02 (Filipe, 2011) to calculate allelic richness for combinations of island populations, standardized by the smallest combined sample size in each case. This method provides highly precise and unbiased estimates of the allelic richness with statistical power to detect differences in variation (Leberg, 2002). Mean allelic richness and standard deviation were calculated from 10 replicates of random subsampling for each possible combination of *k*. Allelic richness of all combinations of *k* islands was ranked for each species to obtain maximum (MaxAR) and minimum (MinAR) allelic richness for each *k*.

Assessing the potential adaptive variation value of island subsets

We incorporated potentially adaptive variation into our analyses using a phenotypic divergence matrix based on five morphological measurements (wing and tarsus length, bill length, depth and width) for each *Zosterops* species to quantify differences among islands (see Phillimore *et al*. 2008, Clegg & Phillimore, 2010). These morphometric traits have often been found to have a heritable component in birds (Merilä & Sheldon, 2001) and some traits have been shown to be heritable in another island *Zosterops* population (Frentiu *et al.*, 2007; Clegg *et al.*, 2008). For each species, we calculated the total phenotypic divergence (PD) protected by selecting a given combination of *k* islands out of *n* following the same procedure described above, but using the phenotypic divergence matrix instead of the genetic divergence matrix (Suppl. Figs.S4 and S5 for *Z. flavifrons* and *Z. lateralis*, respectively). Values were ranked to produce maximum (MaxPD) and minimum (MinPD) phenotypic divergence for each *k*. For *Z. lateralis*, two island populations (Ambae and Vanua Lava) with small sample sizes (<5) were excluded from the analysis, leaving nine island populations.

Calculating the geographic surrogacy value of island subsets and their respective genetic or phenotypic value

We tested the surrogacy value of three indices: maximising geographic distance between islands (farthest islands, henceforth, FI, measured in km) and maximising the area of islands (henceforth, area, measured in km^2), both calculated in ArcGis version 9.3 using the ESRI

country layer, and maximising geographic representation of islands (henceforth, MR). . Geographic distance was expressed as a matrix of pairwise linear distances from the centroid of each island's polygon to all other islands' centroids. Area was expressed as a list of each island's polygon area. To calculate the geographic surrogacy value of subsets of FI (Suppl.Fig.S7), we followed the previously described approach, but using the geographic distance matrix of the islands to generate the tree (Suppl.Fig.S6).

Islands were ordered by area and the set of islands that maximized summed area for each *k* were identified; e.g. for*k*= 2 summed values for Espiritu Santo (4097 km^2) and Malekula (2140 km^2). MR islands were identified using the geographic distance tree (Suppl.Fig.S6) to find the combination of *k* islands that minimised the branch lengths' sum between a selected island and the remaining unselected islands using eq. 2. (*sensu* Faith, 1992; Faith & Walker, 1996), (Suppl.Fig.S7):

$min \sum_{k' \in K'}^{n} (\left[d_{k', k \in K'} \right])$, where (2)

K' is a set of nearest neighbour *k'* islands.

For each of the surrogates (FI, Area and MR), we extracted the corresponding, directly-measured genetic values for all combinations of islands at each *k*. This dataset consisted of the maximum and minimum genetic values measured directly for between population divergence (referred to MaxGV and MinGV, respectively), and within population diversity (MaxAR and MinAR, respectively) and maximum genetic divergence obtained from using the FI sets of islands, the genetic diversity obtained from using the largest islands (area) and the MR set of islands. Similarly, for phenotypic divergence we produced a dataset of maximum (MaxPD) and minimum (MinPD) phenotypic divergence measured directly from the phenotypic data protected when selecting the islands using all three geographic surrogates for each *k* set of islands.

Testing performance of the geographic surrogacy values

We tested the performance of surrogates by comparison to values from sets of randomly selected islands. For each *k*, 1000 random set of islands were drawn. At each iteration genetic

divergence and diversity and phenotypic divergence were calculated as described previously. The averages and 95% confidence intervals were calculated across all iterations.

Results

Genetic and phenotypic values of subsets of islands

MaxGV and MinGV recovered from choosing a *k*-number of island populations are shown for the two pairwise genetic distance measurements of *Z. flavifrons* (Fig. 2a,b) and for pairwise F_{ST} of *Z. lateralis* (Fig. 2c). When more islands were selected, more genetic divergence was captured for both mtDNA and microsatellites (Suppl.TableS1a). Genetic divergences protected for *Z. lateralis* were consistently higher than for *Z. flavifrons* at each *k* (Fig. 2b, c, Suppl.TableS1a). For example, in *Z. lateralis*, the four most genetically divergent populations captured over 97% of genetic variation based on microsatellites, compared to 64.6% for *Z. flavifrons*. The results for *Z. flaviforns* analysed by plumage colour, are presented in Appendix 2.

The directly measured allelic richness for both species also increased as more islands were selected (Suppl.Table S1b, Figs. 3a,b). However, the accumulation of allelic diversity with the addition of islands asymptoted faster in *Z. lateralis* than *Z. flavifrons* (Fig. 3b, Suppl.Table S1b). Around 84% of *Z. lateralis* allelic richness could be protected by selecting two islands, compared to just over 68% in *Z. flavifrons* (Suppl.Table S1b). This reflects the difference in regional genetic population structures of both species. The addition of extra *Z. lateralis* populations does not dramatically increase allelic diversity. Alleles are more likely to be shared due to the high gene flow among most *Z. lateralis* populations . In contrast, *Z. flavifrons* populations are less influenced by gene flow, resulting in restriction of some alleles to particular populations, therefore, addition of islands increases allelic richness in generally larger increments.

Phenotypic divergence for each species increased with addition of island populations (Fig. 4 a, b, Suppl.Table S1c; and Suppl.Table S2c). The percentage of phenotypic divergence protected for *Z. lateralis* was consistently higher than for *Z. flavifrons* for a given *k* (Suppl.TableS1c). Again, this reflects higher average phenotypic divergence of *Z. flavifrons* populations compared to *Z. lateralis* populations (Suppl.TableS1c P_{ST}), and therefore slower accrual of phenotypic divergence when expressed as a percentage of the total.

Geographic surrogates for among-population genetic divergence

Genetic divergence obtained by selecting islands based on FI, MR or at random were all below the MaxGV extracted directly from the genetic data for both species for all *k*-values (Fig. 2 a-c, Suppl.Table S1a). The success with which surrogates (compared to random selection) captured genetic divergence varied depending on species, genetic markers and number of islands selected. Choosing two furthest apart islands captured nearly 45% of mtDNA divergence and 30% of microsatellite divergence in *Z. flavifrons*, and 56% of microsatellite divergence in *Z. lateralis*. The MR sets of islands retained a minimum of 4% of mtDNA divergence and 6% of microsatellite divergence in *Z. flavifrons*, and 9% of the total microsatellite divergence in *Z. lateralis*. Random selection captured around 28% for mtDNA and 21% of microsatellite divergence in *Z. flavifrons*, and 28% of total microsatellite divergence in *Z. lateralis* (Suppl.Table S1a).

In *Z. flavifrons*, greater deviations from MaxGV were observed when using the microsatellite dataset compared to mtDNA dataset (Fig. 2b, Suppl.Table S1a). The best surrogate for mtDNA divergence was to use FI when $k \leq 6$, but to choose the MR islands when $k \geq 7$. Choosing islands randomly never produced the highest mtDNA genetic divergence, however, random selection outperformed FI (but not MR) for $k = 7,8,9$ and 12 and MR (but not FI) for $k \leq 6$. Identifying the best geographic surrogate for *Z. flavifrons* based on microsatellite divergence was less clear. When $k \leq 3$ and $k \geq 12$, the FI surrogate performed best. The MR set of islands tended to be best when $k=6$ and $8 \leq k \geq 11$, however, random selection performed best when $k=4$, 5 and 7. In addition random selection outperformed MR (but not FI) when $k \leq 3$, and outperformed FI (but not MR) when $k=6$ and $8 \geq k \leq 11$. The best performing geographic surrogate for *Z. lateralis* microsatellite divergence was to use FI when $k \leq 4$, but to choose the MR islands when $k \geq 5$. Random island selection for *Z. lateralis* was less effective than using at least one of the geographic surrogates across all values of *k*. However it outperformed MR (but not FI) for $k=2$ and 4 and FI (but not MR) for $k= 6$ and 7.

Geographic surrogates for within-population genetic diversity

Geographic surrogates of island area and MR did not capture the full degree of genetic diversity based on allelic richness, and their effectiveness varied depending on species and number of islands selected. Choosing the largest islands captured 64% of MaxAR for *Z.*

flavifrons, and 72% of MaxAR for *Z. lateralis* (Fig. 3; Suppl.Table S1b). This compares to the minimum 45% and 77% respectively for the MR islands. Random selection captured 52% of MaxAR in *Z. flavifrons*, and 75% in *Z. lateralis* (Suppl.Table S1b).

Area proved the best geographic surrogate in *Z. flavifrons*, when $k \leq 5$ and MR was best when $k \geq 7$. At medium values of k ($6 < k < 8$ where the highest number of combinations is possible) the discrepancy between actual allelic richness and that captured using the area surrogate widened (Fig. 3a, Suppl.Table S1b). It is interesting to note that the closest representation of MaxAR using an area surrogate to the actual allelic diversity for *Z. flavifrons* occurred at $k = 2$ and $k = 12$. Choosing the two largest islands would capture 93% of the actual MaxAR (69% of the total diversity). For *Z. lateralis*, there was little consistency in performance of surrogates, with the best result alternating among area, MR and random selection (Suppl.Table S1b). Area was the best surrogate only when $k > 7$, while MR worked best for $k = 2$ and k=5 and 6. (Fig.3; Suppl.Table S1b). Random choice of islands returned the highest percentage of protected variation at $k = 3$ and 4 (Fig. 3 and Suppl.Table S1b).

Geographic surrogates for phenotypic divergence

As with genetic divergence, the best geographic surrogates for capturing phenotypic divergence varied by species and the value of *k*. Choosing sets of FI captured a minimum of 26% of phenotypic variation in *Z. flavifrons* and 34% in *Z. lateralis* (Suppl.Table S1c). For MR, the corresponding percentages were around 19% for all *Z. flavifrons* and 14% for *Z. lateralis*.

In *Z. flavifrons*, choosing the FI performed best when $k \leq 5$ and $k = 12$, MR performed best for $k = 6$, 8, 9 and 10. Random selection performed best at $k = 7$ and 11, but also performed better than FI (but not MR) at $k = 6$ and $k = 8$ to 10, and better than MR (but not FI) when $k \leq 5$ and $k = 12$ (Fig. 4a; Suppl.Table S1c). In *Z. lateralis*, choosing the FI was the better geographic surrogate for MaxPD (Fig. 4b; Suppl.Table S1c) for all k except $k = 7$, when MR was the best surrogate. Random selection of islands was never the best performer, but outperformed MR (but not FI) when $k \leq 4$ (Fig 4b; Suppl.Table S1c).

Discussion

Conservation plans accounting for genetic variation targeting evolutionary significant units instead of species are more cost-effective in preserving evolutionary processes (Vasconcelos *et al.*, 2012). Assessing genetic variation for conservation can be expensive and time-consuming, therefore surrogate measures of variation are worth exploring. We expected that differences in regional population genetic structure of the species' considered here, would influence performance of the different geographic surrogates. FI was expected to capture genetic and phenotypic divergence effectively for *Z. lateralis*, a more recent colonizer, with strong signatures of distance-mediated gene flow across the archipelago (Clegg & Phillimore, 2010). Island area, as a proxy for population size, was expected to perform well for *Z. lavifrons*, as their populations show a weaker influence of distance-mediated gene flow with drift also affecting divergence (Clegg & Phillimore, 2010).

The effectiveness of easily obtainable geographic surrogates to capture intraspecific genetic and phenotypic variation in two species of island-dwelling birds was variable. We did not identify a single surrogate performing consistently better for both species, or indeed one which performed consistently better than random across all numbers of selected islands within each species. Still, important generalisations can be drawn from our results. FI represented genetic and phenotypic divergence better when protecting less than 50% of island populations of both species, except for *Z. flavifrons* microsatellite divergence. Therefore, despite the difference in regional population structures of the two species, FI was useful for capturing the most divergent populations at least at smaller values of *k*.

When protecting more than 50% of islands, choosing the MR sets was often a better surrogate for capturing genetic and phenotypic divergence among populations. This may result from maintenance of connectivity between populations while maximizing the depth of the genetic diversity. As conservation targets can usually only protect at most 50%, of remaining populations (McDonald-Madden *et al.*, 2008), our results suggest that in systems with suspected gene flow, FI would be the surrogate of choice for maximising between population divergence in the absence of detailed empirical studies. The geographical positioning of islands or fragments may be another important factor to consider, as under a less linear arrangement of islands, MR may perform well at low values of *k*.

Interaction of spatial arrangement and islands' size may cause a trade-off in capturing within versus between population diversity. Highly divergent populations with high within-

451 population variability would capture more diversity than populations with low divergence
452 and low variability. Although often highly divergent populations are genetically depauperate
453 (e.g. small peripheral populations), and large populations with low divergence have higher
454 within population diversity (e.g. large central populations connected by high levels of gene
455 flow). In archipelagos with roughly linear spatial arrangement, using FI and MR surrogates
456 will result in selection of peripheral and central islands, respectively. Where central islands
457 are relatively large and the peripheral relatively small, as in Vanuatu, FI is unlikely to
458 simultaneously maximize within and between population variation, whereas MR will fail to
459 capture the most divergent peripheral populations.

460 The crucial factor when maximising within- population genetic diversity is effective
461 population size: rare alleles' loss via drift is more likely in small populations (Wright, 1943;
462 Futuyma, 1986). We expected that island size (as proxy for population size) would be an
463 appropriate surrogate for genetic diversity, particularly where all gene flow among
464 populations has ceased, and diversity within populations is mediated by genetic drift (and
465 input from new mutations over very long timescales) (Jordan & Snell, 2008). The difference
466 in effectiveness of area as a surrogate for within-population diversity in both species was
467 consistent with this expectation; area performed well at least for lower values of *k* in *Z.*
468 *flavifrons*, but was not the best geographic surrogate for Z. *lateralis*. This may be explained
469 by the complex dynamics of gene flow in the Z. *lateralis* system, including large asymmetries
470 in gene flow direction, and potential influences of population size on levels and direction of
471 gene flow (Clegg & Phillimore, 2010).

472

473 **Further avenues & limitations**

474 Combining several surrogates may enhance the benefits for genetic and phenotypic variation
475 and may even serve to maximise evolutionary potential of protected populations (Weigelt &
476 Kreft, 2013). Island biogeography studies have improved our understanding of how
477 evolutionary processes structure morphological and genetic diversity within and between
478 fragmented populations (e.g. Heaney, 2007). For example, the rate of speciation on islands
479 increases with island size, island age, topographical and habitat diversity, ecological and
480 geological features and with island's isolation (e.g. Whittaker *et al.*, 2008; Losos & Ricklefs,
481 2009; Wilson *et al.*, 2009; Kisel & Barraclough, 2010; Vasconcelos *et al.*, 2010). These
482 factors could be correlated with each other, as larger or intermediate age islands tend to have

483 greater habitat/topographic diversity (MacArthur & Wilson, 1967; Kirchman & Franklin,
484 2007).
485
486 The degree to which these same surrogates would be useful when targeting variation in taxa
487 (e.g. amphibians, reptiles, mammals, insects) provides a further line of enquiry. Divergence
488 metrics may work best for species that maintain a gene-flow mediated population structure,
489 e.g. some bird species or flying insect species. More sessile organisms or those with limited
490 dispersal capacity could tend to have more of a drift-mediated population structure with little
491 gene flow among populations (Kisel & Barraclough, 2010) and therefore diversity metrics
492 may perform better. Island biodiversity patterns within-species are broadly dictated by the
493 same biogeographical processes although the scale at which these processes occur may be
494 very different across taxa (Whittaker *et al.*, 2008). There is not a feasible method to test if
495 regional population structure is gene-flow or drift mediated without doing direct genetic
496 analyses. For species with expected high levels of gene flow between populations, ensuring
497 the maintenance of gene flow between conserved islands is very important. This may
498 necessitate preservation of some habitat in intervening islands or fragments that facilitate
499 gene flow. Assessing the applicability of our method across multiple taxa including recently
500 fragmented continental populations requires further examination.
501
502 In some cases, geographic surrogates such as FI might not be an appropriate approximation
503 of genetic and phenotypic variation. For example in populations fragmented very recently the
504 time required to re-establish a regional population genetic structure may delay a relationship
505 between divergence measures and geographic distance (Tamura *et al.*, 2007). In other cases,
506 complete population isolation over a long evolutionary timeframe could eliminate any
507 relationship between geographic distance and genetic divergence. Other processes that might
508 affect this approach's utility include asymmetrical migration rates (e.g. source-sink
509 dynamics), local adaptation, or differences between mtDNA and microsatellites concordance
510 estimates. Geographic isolation may not result in much phenotypic divergence if
511 environments (and therefore selection regimes) are very similar. Neutral divergence will
512 accrue in the absence of gene flow. Hence, maximizing physical or ecological distinctiveness
513 (whenever data is available) of islands as well as geographic measurements would improve
514 the genetic variability protected using geographic surrogates.

Without previous knowledge of population genetic structure, planners may be reluctant to use geographic surrogates. However, delaying the decision while data are gathered may lead to lost opportunities for conservation. Conversely, insufficient prior knowledge may lead to poor decisions (Possingham, 2007; Black, 2010). Hence we do not argue that genetic studies are not desirable to improve conservation decisions (Leberg, 2002), and instead suggest planners analyse the trade-off between time and money required to gain genetic information and the benefits those data can provide relative to an immediately available surrogate.

In conclusion, for simple geographic surrogates to be effective conservation tools they must indicate an underlying trait, and be easily and rapidly assessable. Simple and easily obtained surrogates or combinations of surrogates would be a significant step forward for threatened species management on islands, given the limited financial resources and the urgency of most conservation actions. Our analyses show that there is no simple best surrogate across all the scenarios examined, but a combination of surrogates may improve the outcome. In the absence of directly gathered population-level information, maximising geographic distance among conserved populations (especially for small numbers), serves as an attainable, though imperfect surrogate under a range of scenarios.

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722

Figure Legends

Fig. 1:Major islands of the Vanuatu archipelago, located in southwest Pacific region (inset). The endemic *Zosterops flavifrons* is found on all of the 13 major islands. The islands where the dark plumage group occurs are in dark grey, and the islands where the yellow plumage group occurs are in light grey. Black triangles mark the islands where *Z. lateralis* also occurs. Labelled islands were sampled:
A - Vanua Lava; B – Gaua; C - Espiritu Santo; D – Maewo; E – Ambae; F – Pentecost; G – Malekula; H – Ambrym; I – Epi; J – Efate; K – Erromango; L – Tanna; M – Aneityum.

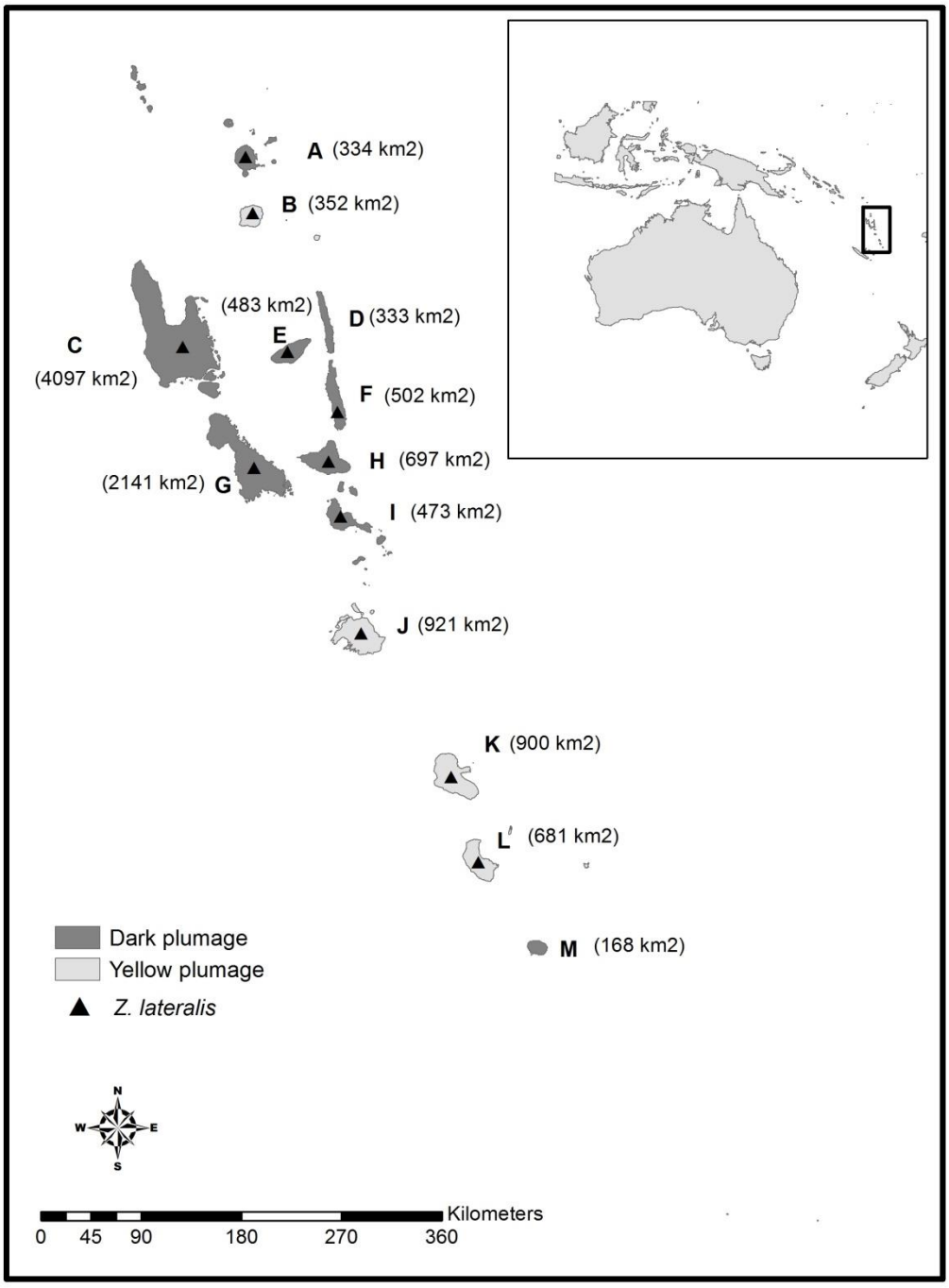
Fig.2: Changes in the genetic divergence (GV) protected using geographic distance between islands as surrogates of genetic variation for each metric when selecting *k* number of islands for conservation: a) Pnet- distance of *Z. flavifrons*, b) pairwise F_{ST} of *Z. flavifrons*; and c) pairwise F_{ST} of *Z. lateralis*. Performance curves are shown for the maximum (MaxGV) and minimum (MinGV) genetic value captured when using genetic data directly, and the genetic value protected when selecting subsets of islands furthest apart (FI), subsets of islands representing the geographically most representative set of islands (MR) and random island selection (Random).

Fig. 3: Changes in genetic diversity (GV) protected (as allelic richness) when selecting *k* number of islands for conservation: largest area size of islands (area), and islands most representative of the geographic space (MR) for a) *Z. flavifrons* and b) *Z. lateralis*. Performance curves are shown for the maximum (MaxAR) and minimum (MinAR) genetic value captured when using genetic data directly, and the genetic value protected when selecting subsets of islands furthest apart (FI), subsets of islands representing the geographically most representative set of islands (MR)and random island selection (Random).

Fig.4: Changes in phenotypic divergence (PD) protected when selecting *k* number of islands for conservation for a) *Z. flavifrons* and b) *Z. lateralis*. Performance curves are shown for the maximum (MaxPD) and minimum (MinPD) amount of phenotypic divergence protected by measuring the phenotypic divergence directly, when selecting subsets of islands furthest apart (FI), subsets of islands representing the geographically most representative set of islands (MR)and random island selection (Random).

757 **Fig. 1.**

758



759

760

Fig. 2

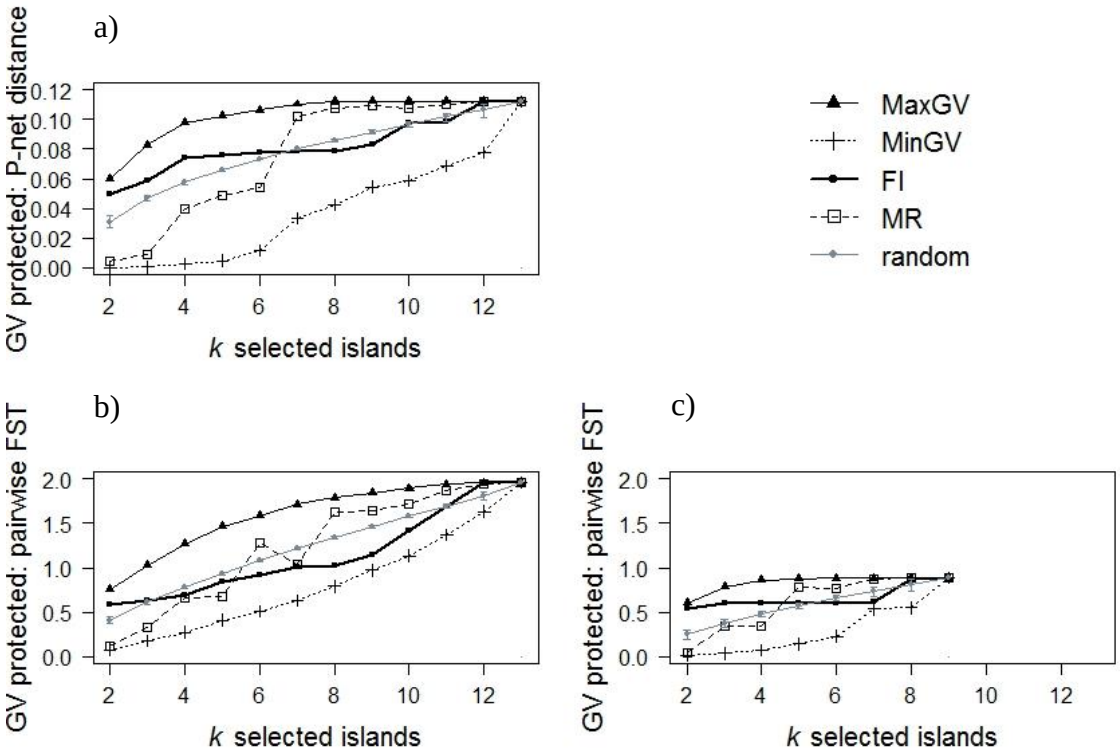

a)
GV protected: P-net distance
0.00
0.02
0.04
0.06
0.08
0.10
0.12
2
4
6
8
10
12
k selected islands
MaxGV
MinGV
FI
MR
random
b)
GV protected: pairwise FST
0.0
0.5
1.0
1.5
2.0
2
4
6
8
10
12
k selected islands
c)
GV protected: pairwise FST
0.0
0.5
1.0
1.5
2.0
2
4
6
8
10
12
k selected islands

Fig. 3

a) b)

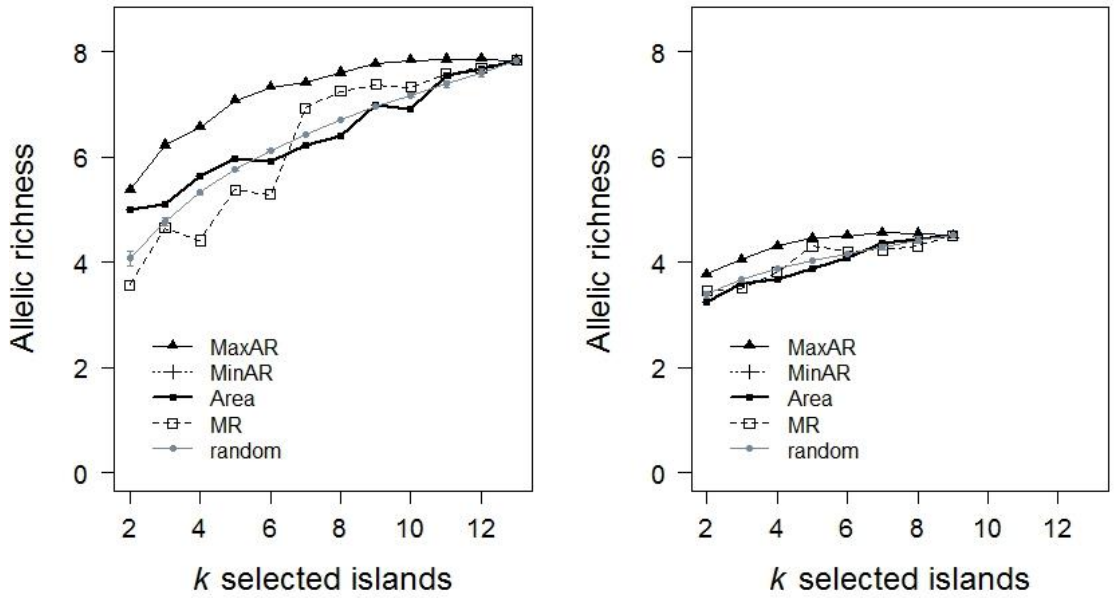
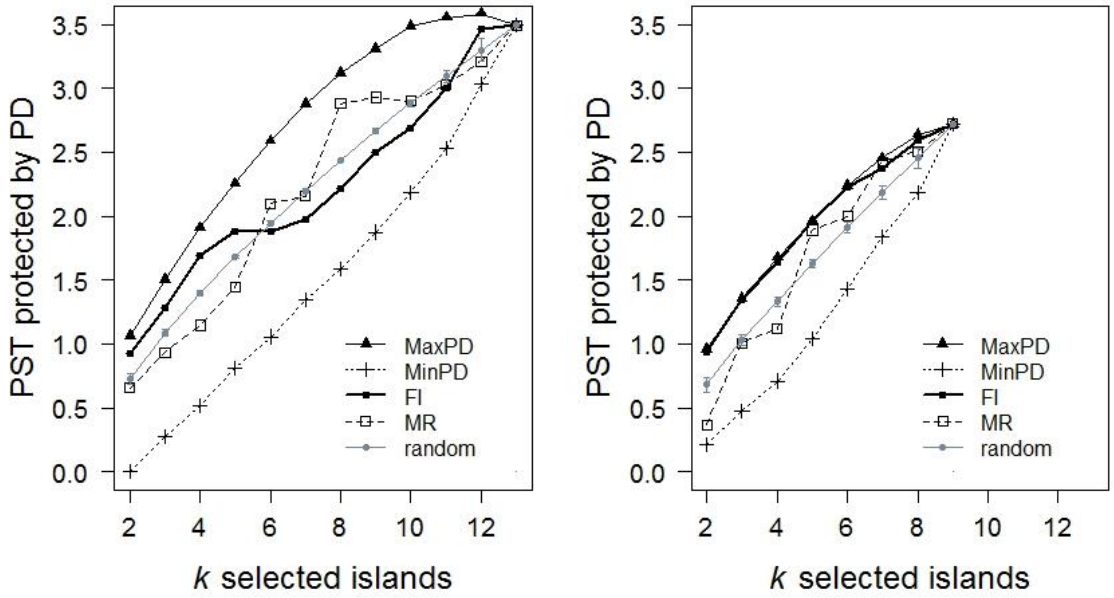


Fig. 4

a) b)



Biosketch

This study was part of Rocío Ponce-Reyes's PhD project, focused on the integration of evolutionary processes in conservation planning. Rocío's main research interest is improving conservation planning strategies in a dynamic environment through the inclusion of ecological end evolutionary processes.

Contributions by authors:

- All the authors designed the study during a workshop held at The University of Queensland
- RPR and SBC performed the analyses
- SMC provided the data and analysed results
- RPR and SMC wrote the first draft of the manuscript
- All the authors contributed substantially to revisions.