Ecography 38: 96–107, 2015
doi: 10.1111/ecog.00793

Subject Editor: Jose Alexandre Felizola Diniz-Filho. Accepted 28 April 2014

Increasing rate of species discovery in sharks coincides with sharp population declines: implications for biodiversity

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The global biodiversity of some taxonomic groups is poorly described, but thought to be decreasing rapidly. Surprisingly, this holds for a group of the world's most iconic large-bodied animals: sharks. Our analysis shows rapid and steep contemporary population declines in sharks coinciding with an increasing rate in species discovery. Larger sharks occupying lower trophic positions with wide geographic distributions (latitudinal ranges) found in shallow waters tend to be discovered first. In light of this increasing trend in species discovery and a cumulative description record far from reaching an asymptote, models cannot predict the global number of sharks. Our results highlight that while our knowledge of shark diversity improves at an accelerating rate, this diversity is under threat and declining rapidly; most shark species are vulnerable to declines, especially smaller-bodied sharks. This surprising finding may relate to mesopredator declines following periods of rapid expansion due to the demise of large sharks (apex predators). Furthermore, shark population declines are structured by phylogeny and, to a lesser extent, geography. Decline in sharks are likely to influence other species as well, e.g. via trophic cascades. The net result may be a greater loss of biodiversity in the oceans and could potentially explain why fewer extinction events are observed than predicted by models. Likewise, it is not inconceivable that species may be lost prior to their discovery.

Current estimates of global biodiversity are difficult to obtain (Wilson 2003a), but range between 3 and 100 million species (May 2010). Wilson (2003b) places this number closer to ten million, with fewer than 20% of these, considered by some a generous estimate (Mora et al. 2011), having been described. Yet, we are currently faced with a biodiversity crisis stemming from anthropogenic sources, such as overexploitation, habitat conversion, biotic invasions, contamination and climate change (Sala et al. 2000, Magurran and Dornelas 2010). Rapid population declines and extinctions have been reported worldwide (Brook et al. 2003) with current rates far exceeding historical ones (Pimm et al. 1995, May 2002). Given the current anthropogenic pressures placed on biodiversity, it is predicted that we will lose over 50% of species within the next half century (Pimm and Raven 2000, Thomas et al. 2004).

In the oceans, there are widespread declines of top predators, particularly sharks (Graham et al. 2001, Baum et al. 2003, Myers and Worm 2003), with some populations declining by over 99% (Baum and Myers 2004, Ferretti et al. 2008). The primary culprit is human overexploitation through direct and indirect effects of fisheries (Baum et al. 2003, Dulvy et al. 2008, Ferretti et al. 2008). Since sharks are generally late maturing, slow growing, and have low fecundity, compared to teleosts, they are particularly vulnerable to fishing mortality (Musick et al. 2000, Stevens et al. 2000, Frisk et al. 2001, Myers and Worm 2005). In fact, the ability of sharks to recover after depletion is low (Smith et al. 1998, Stevens et al. 2000), and they are twice as likely to go extinct as commercially exploited teleosts (Myers and Worm 2005).

Removal of sharks from communities can have complex and unpredictable consequences (Stevens et al. 2000) including community restructuring (Ward and Myers 2005, Myers et al. 2007, Ferretti et al. 2010). Removing sharks from communities can cause an overall decrease in omnivory and induce trophic cascades, reducing ecosystem resilience (Bascompte et al. 2005). Examples include the collapse of the bay scallop fishery in the northwest Atlantic (Myers et al. 2007) and the degradation of the Caribbean marine ecosystem (Bascompte et al. 2005). Understanding such consequences of changes in biodiversity is imperative to address issues relating to ecosystem function, resilience and stability (Dornelas et al. 2013). Thus, with nearly a third of chondrichthyans assessed by the IUCN considered threatened or near-threatened (Camhi et al. 2009), it is imperative to better understand changes in shark biodiversity and their respective roles in marine communities.

Despite declines of sharks, new shark species are being described at an increasing pace since 2000 (Last 2007, White and Last 2012). In free-living organisms, body size and geographic range are important correlates of species discovery (Gaston 1991, Blackburn and Gaston 1995). The inverse relationship between a body size and the year of its discovery is observed in many taxa (Gaston 1991, Gaston and Blackburn 1994, Blackburn and Gaston 1995, Ferro and Diniz 2008), although not universal (Reed and Boback 2002, Gibbons et al. 2005, Ferro and Diniz 2008). Also, species occupying a wider geographical range are more likely to be discovered earlier than those with more restricted ranges (Blackburn and Gaston 1995, Gaston et al. 1995, Allsopp 1997, Collen et al. 2004, Zapata and Robertson 2007, Baselga et al. 2010, Trotta-Moreu and Cabrero-Sanudo 2010). Other variables identified as influencing discovery include: abundance (Blackburn and Gaston 1995), altitudinal range (Blackburn and Gaston 1995), colouration (Ferro and Diniz 2008), and depth (Gibbons et al. 2005).

Current discovery rates of shark species have not been carefully studied (but see Last 2007), nor has this been contextualised within the extent and rate of shark population declines. As of September 2012, there were nearly 500 described species of sharks with broadly ranging characteristics: 1) size range of between 12 cm (the Indonesian wobbegong *Orectolobus leptolineatus*) and 21 m (the whale shark *Rhincodon typus*) (Froese and Pauly 2012); 2) distributed in all of the world's oceans; 3) distributed over 85% of the latitudinal scale; 4) encountered over a vast range of depths; and 5) covering all marine habitats. The objectives of this study are to: a) quantify the current species description rate in sharks and draw historical comparisons; b) estimate the global shark biodiversity; c) identify factors influencing the discovery of these fishes; and d) calculate the contemporary rates of decline in shark populations. Our results highlight that while our knowledge of shark diversity improves at an accelerating rate, this diversity is dwindling rapidly, with smaller shark species more vulnerable. Additionally, there is a strong phylogenetic, and to a lesser extent geographic, structure to these declines.

Material and methods

The dataset

The complete list of valid described shark species (accounting for known synonyms) was compiled in September 2012 using Compagno (1999), Compagno et al. (2005), and FishBase (Froese and Pauly 2012). Web of Knowledge was used to identify records published after 2005 and as a means to confirm information on FishBase. Since there is a time lag of several months between papers being published and their availability on the Web of Knowledge, species descriptions published after December 2011 were discarded to ensure an exhaustive complement of species for each year included in our analyses. For each shark species, using FishBase (Froese and Pauly 2012) we compiled: 1) year of description; 2) Order; 3) Family; 4) Genus; 5) maximum body length (total length); 6) latitudinal range; 7) depth range; 8) mid-point of the depth range; and 9) trophic level (Supplementary material Appendix 1). Owing to the lack of data, we were unable to assess the influence of numerical abundance on discovery year. Furthermore, sharks that are brightly coloured or displaying colouration contrasting with that of the water may be more likely to be discovered prior to those more cryptically-coloured. However, due to the subjective nature of colour measurements and the intraspecific variability of colouration in sharks, this trait was omitted from our analyses. Additionally, a table summarising localised changes in shark abundance over time was compiled through the ISI Web of Knowledge, searching through all databases, using (population* AND [change OR increase* OR declin*] AND shark*) in August 2012 (Supplementary material Appendix 2). Of note, this search was repeated in August 2013 by substituting 'shark*' with individual shark genera (Supplementary material Appendix 2). Only records identifying a locality/region, a time period for which the population abundance changed, and quantified population change were included in our table and analyses. When records were collated from supplementary material accompanying a publication (Myers et al. 2007), i.e. not subjected to the process of peer-review, only records showing a statistically significant trend were included in the table and subsequent analyses. Additionally, an index of human impact was obtained from Halpern et al. (2008) for each corresponding locality and included in analyses.

Statistics

Discovery rates for each year correspond to the difference in number of species described in consecutive years: $S\ (t+1) - S\ (t)$, where S corresponds to the number of new shark species described each year. We calculated the average discovery rate and 95% confidence intervals using generalized linear models with quasipoisson error to accommodate the overdispersed and discrete nature of the data. This rate was calculated for the entire dataset (1758–2011) as well as for the distinct periods corresponding to: 1) 1758 to World War (WW) I; 2) period between both WWs; 3) post-WWII to molecular era (1985); and 4) molecular era to 2011. In a wide range of taxa, the rate of species discovery is known to decline during both WWs, and for up to several years later (Costello and Wilson 2011). For this reason, periods corresponding to each WW + 4 yr (1915–1922 and 1940–1949) were excluded from our divided dataset. Furthermore, since papers discovering new species in the year preceding each WW may appear in print in 1914 and 1939, these 2 yr were not excluded.

To estimate the total number of species we adopted the approach of Bebber et al. (2007), who use a generalized linear model with quasipoisson error to fit the model $E(S_t) = k(\mathrm{N}_{tot} - \mathrm{N}_{t-1})$, where $E(S_t)$ is the expected number of species discovered in year t, N_{tot} is the total number of species, N_{t-1} is the cumulative number of species described by year $t-1$, and k is a parameter to be estimated. We also considered a non-linear form for k, where $k = b + c\ \mathrm{N}_{t-1}$ (Bebber et al. 2007).

Additionally, to identify factors influencing year of discovery in sharks (dependent variable), generalized linear mixed models (GLMM) with Gaussian error distribution and identity-link function (with Total length, Latitudinal range, Depth range, and Mid-point of the depth range on log scales and Trophic level as fixed effects and shark Genus nested within Family nested within Order [Genus:Family:Order] as a random effect) and multi-model inference approaches were performed on species for which all data were available ($n = 381$ species) using the package MuMIn ver. 1.9.11 (Barton 2013) in the program R (R Development Core Team). Quantification of phylogenetic influences on year of discovery was achieved using the proportion of the variance explained by the random effect in the intercept model.

Annual rates of population changes were calculated using an exponential population growth rate model applied to observations on the population change (%) over a time period T. The average population growth rate can be estimated as $r = \ln(1 - x)/\mathrm{T}$, where $1 - x$ corresponds to the observed change in abundance expressed as a proportion. The annual change (%) per population is therefore $(1 - \exp(r)) \times 100$. Factors influencing the annual population change (dependent variable) were identified using GLMM with Gaussian error distribution and identity link function. Log Total length, Log Latitudinal range, Log Depth range, Log Mid-point of the depth range, Trophic level, and index of Human impact were selected as fixed effects, and shark Family and Geographical locality as a random effects) and multi-model inference approaches (see above) on species for which all data were available ($n = 94$ observations; 45 species from 26 genera, 15 families and 6 orders; 9 different localities). Here, geographical locality corresponds to the body of water where data were collected from, i.e. Gulf of Mexico, northwest Atlantic, Mediterranean Sea, etc. Several shark species included multiple *r*-values (Supplementary material Appendix 2 and 3), thus shark species (e.g. blue shark, great white shark, etc.) was used as a random effect nested within Genus, nested within Family and nested within Order (Species:Genus:Family:Order). Quantification of phylogenetic influences and geographical locality on population change were assessed using the proportion of the variance explained by these random effects in the intercept model. The index of Human impact was calculated using the weighted average of values provided in Halpern et al. (2008) for a given geographical locality (see Supplementary material Appendix 4 for additional details).

Analyses on annual rates of change were repeated using the phylogenetically independent contrasts (PIC) method (Felsenstein 1985) to control for confounding effects of shared evolutionary ancestry on shark features used in these analyses. Contrasts were computed using the PDAP:PDTREE program (Midford et al. 2005) implemented in Mesquite ver. 2.5 for Mac OSX (Maddison and Maddison 2007). We derived contrasts from a tree generated using an alignment consisting of previously published molecular data for the NADH dehydrogenase subunit 2 (NADH2) (Fig. 1) for 48 shark species and 2 outgroups, consisting of 1041 sites. Sequences were aligned using MacClade 4.07 (Maddison and Maddison 2005). jModelTest 0.1.1 (Guindon and Gascual 2003, Posada 2008) determined the best nucleotide-substitution model for the data. A general time reversible (GTR) with proportion of invariant sites (I) and gamma-distributed rate heterogeneity (G) provided the best fit to the data based on the Akaike information criterion corrected for small sample size (AICc). The dataset was analysed by methods of maximum likelihood (ML) and Bayesian inference (BI). ML and BI were performed using PhyML 3.0 (Guindon et al. 2010) and MrBayes ver. 3.1.2 (Huelsenbeck and Ronquist 2001), respectively. ML analyses were performed using 6 substitution rate categories, G and I set at 0.688 and 0.326, respectively (estimated from jModelTest), tree improvement set at subtree pruning and regrafting (SPR), and 1000 bootstrap replicates. BI was performed using the covarion option according to a $\mathrm{GTR} + \mathrm{I} + \mathrm{G}$ nucleotide substitution model with no initial values assigned and with empirical nucleotide frequencies, 4 separate Markov chains were used to estimate posterior probabilities over 5×10^6 generations, sampling the Markov chains at intervals of 100 generations. The first 12 500 trees were discarded as 'burn-in' then a 50% majority-rule tree was constructed from the subsequent trees. Nodal support was estimated as the mean posterior probabilities (Huelsenbeck et al. 2001) using the sumt command. The trees were rooted on two outgroup taxa, *Notorhynchus cepedianus* and *Chlamydoselachus anguineus* (Naylor et al. 2012).

For PIC, branch lengths used were those estimated by ML and their statistical adequacy verified according to Garland et al. (1992). Prior to performing PIC, we calculated phylogenetic inertia (Pagel's lambda) using the package Geiger (Harmon et al. 2008) in the program R (R Development Core Team) and determined that there was a strong phylogenetic signal. Closer examination of our phylogeny reveals generally weakly resolved or unresolved relationships at the Genus level, but strong support at the Family level (somewhat consistent with our GLMM assessment of phylogenetic influences). We computed contrasts following guidelines suggested by Garland et al. (1992). Several species were represented more than once in the table on average annual rates of change. Rather than creating several polytomies and reducing significantly the degrees of freedom available for analyses, PIC methods were applied to 2 datasets: each consisted of a single rate of change for each species, represented by the lowest and highest value available for each species, respectively.

Results

By the end of 2011, 493 species of sharks had been recognised (Supplementary material Appendix 1). Our data indicate that we are currently in the midst of an increasing rate of shark discovery (Fig. 2 and Table 1) coinciding with sharp population declines (Supplementary material Appendix 2 and 3). On average, since 1758, fewer than two species of sharks were described per annum compared to nearly five per annum since 1986; or nearly eight per annum since 2000 (Table 1). Historically, rates of shark discovery have been linear (Fig. 2). However, more recently, these have been increasing consistently and the cumulative frequency distribution curve for sharks is far from reaching an

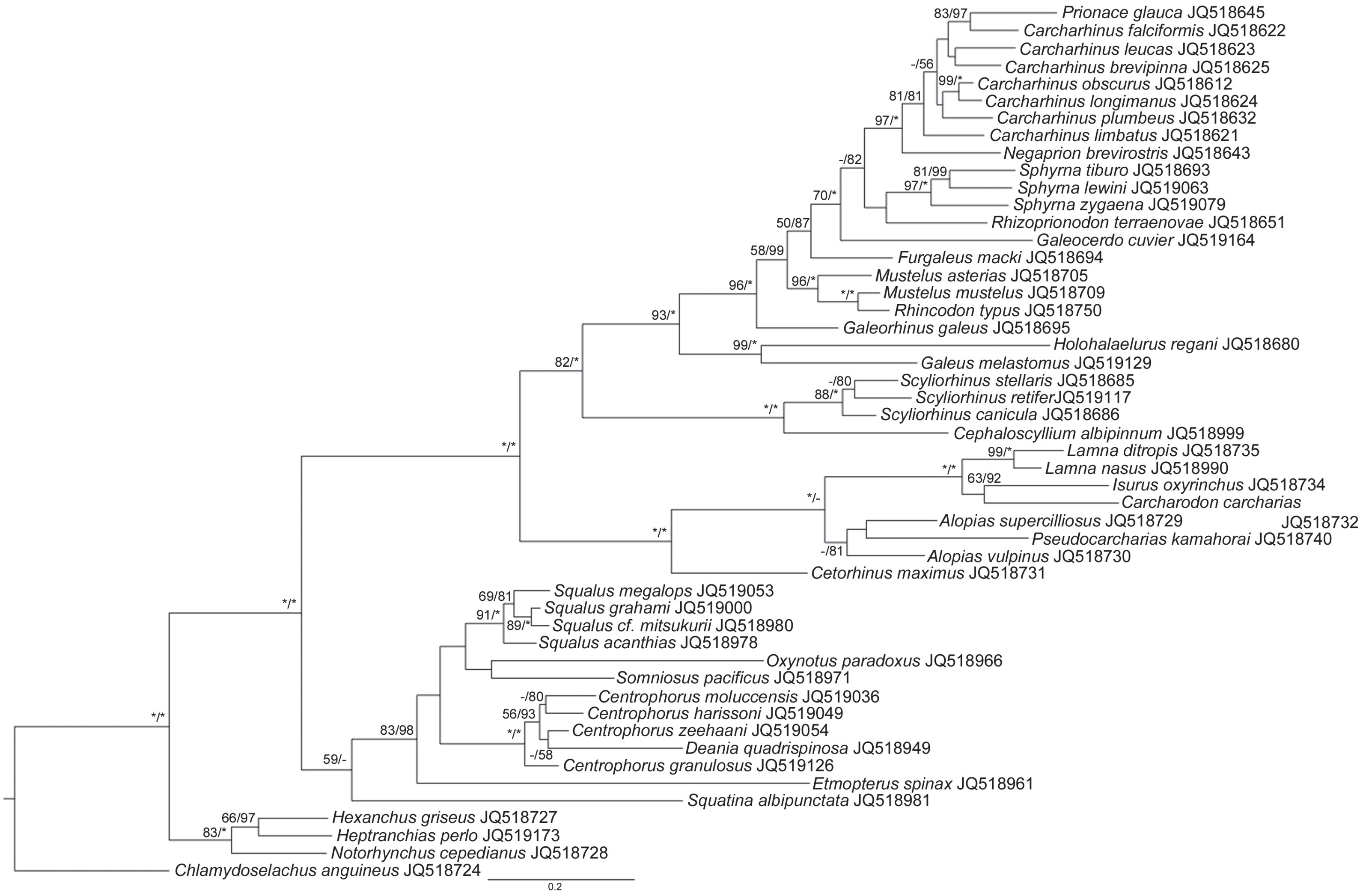

Figure 1. Shark phylogeny generated in this study from which contrasts were derived for phylogenetic independent contrast analyses. Numbers next to species names correspond to GenBank accession numbers for individual NADH2 sequences.

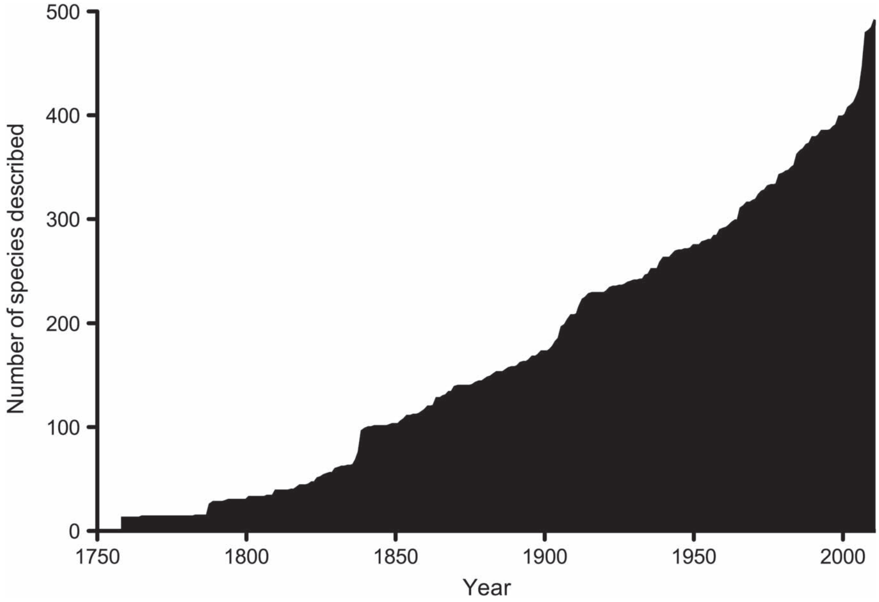

Figure 2. Cumulative frequency distribution of currently recognised shark species (n = 493). Large increases in number of species described correspond to contributions by: Müller and Henle (15 species described in 1838 and 1839) and Last et al. (40 species described in 2007 and 2008).

asymptote (Fig. 2), which indicates many more species to be discovered. However, these trends are not consistent across all shark families. For instance, no lamnid shark has been described in the molecular era (Table 1).

The relationships between S_t and N_{t-1}, and S_t and year, show increasing trends, with the rate of species discovery currently near its maximum and increasing (Fig. 3a and b; respectively), and therefore it was not possible to estimate the total number of shark species, using the adapted Bebber et al. (2007) models. It is obvious, that for sharks, we are currently in the midst of a phase of maximum species discovery; nowhere near saturation.

From the GLMM analyses, we found that taxonomy (shark Genus:Family:Order) explained 16.08% of the variance in year of discovery (Table 2). Furthermore, our analyses on year of discovery (n = 381) revealed two plausible models within 4 ΔAIC_c of each other corresponding to 0.99 Akaike weights (w_i). The 'best' model all five fixed effects (Total length, Latitudinal range, Depth, Mid-point of depth range, and Trophic level) ($w_i = 0.82$). The other model included four fixed effects (Total length, Latitudinal range, Mid-point of depth range, and Trophic level) ($\Delta AIC_c = 3.10$; $w_i = 0.17$). Our model averaging approach identified Depth range as a pretending variable (non-informative variable that does not decrease the deviance when included in a model – Anderson 2008) (Table 2). Hence, on the basis of simple linear regression analyses from the raw data (results not shown), shark species described recently, compared to the first described sharks, occupy higher trophic levels, are smaller-bodied (2011 = ca 50 cm; 1758 = ca 245 cm), restricted to narrower latitudinal ranges (2011 = ca 4°; 1758 = ca 125°) and inhabit deeper waters (2011 = ca 355 m; 1758 = ca 75 m).

For reports where the median year of the time range during which changes in abundance were recorded was greater than 1970, average annual rates of shark population change range between −83.7 and +10.2% (median −8.4%); mean of −11.1% (95% confidence interval = −7.8 to −14.6%) (Fig. 4a and Supplementary material Appendix 3) with 19.1% of entries showing an annual increase (Supplementary material Appendix 2). There was a negative relationship between the average annual shark population change and the median year of the time period during which there was an observed change in abundance (r = 0.185 from a linear regression; $F_{1,92}$ 3.25, p = 0.0747) (Fig. 4b). Regressions of standardised contrasts using the PIC method identified three statistically significant trends: 1) using the dataset with the least extreme rates of change per shark species, average annual rate of change was negatively correlated with human impact (Fig. 5a); and using the dataset with the

Table 1. Summary of the historical species discovery rates, i.e. number of new species described annually, (with 95% confidence interval) for sharks and orders with at least 15 described species as of December 2011.

	Historical	pre-1914	1923–1939	1950–1985	1986 to 2011	2000 to 2011
Sharks	1.89 (1.50–2.34)	1.35 (1.00–1.77)	1.47 (0.71–2.64)	2.53 (1.69–3.60)	5.00 (2.77–8.19)	7.83 (3.64–14.41)
Carcharhiniformes	1.04 (0.79–1.33)	0.71 (0.48–1.02)	0.76 (0.34–1.45)	1.47 (0.87–2.30)	2.73 (1.43–4.66)	3.92 (1.54–7.99)
Lamniformes	0.06 (0.03–0.10)	0.05 (0.02–0.12)	0.12 (0.02–0.35)	0.08 (0.02–0.21)	–	–
Orectolobiformes	0.16 (0.10–0.24)	0.15 (0.09–0.23)	0.06 (0.003–0.259)	0.14 (0.04–0.33)	0.38 (0.08–1.07)	0.83 (0.19–2.25)
Squaliformes	0.46 (0.33–0.63)	0.28 (0.17–0.43)	0.35 (0.14–0.72)	0.69 (0.40–1.11)	1.50 (0.68–2.81)	2.25 (0.77–4.96)
Squatiniformes	0.08 (0.05–0.13)	0.06 (0.03–0.12)	0.17 (0.03–0.56)	0.06 (0.01–0.17)	0.23 (0.05–0.62)	0.50 (0.12–1.30)

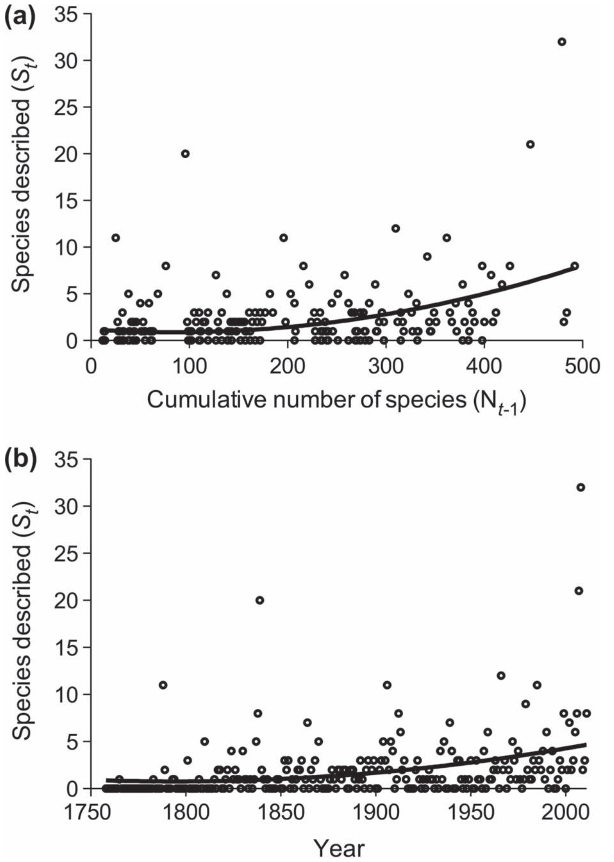

Figure 3. Number of shark species discovered per year (S_t) against: (a) cumulative shark species count to previous year (N_{t-1}) and (b) year. The line represents the best-fit relationship from a non-linear regression (quadratic equation).

most extreme rates of change per shark species, average annual rate of change was negatively correlated with 2) human impact (Fig. 5b); and 3) shark total length (Fig. 5c and 6). From the GLMM analyses, we calculated that shark species (nested within Genus:Family:Order) and Locality explained 74.72 and 3.13%, respectively, of the variance in change in abundance using a null model including both random effects (Table 3). Furthermore, our analyses (n = 94) revealed four plausible models within 4 ΔAIC_c of each other corresponding to 0.73 Akaike weights (w_i) (Supplementary material Appendix 5) and that no model-averaged parameter estimates of fixed effects had a 95% confidence interval bounded away from ‘0’ (Table 3). The null model was 27.05 ΔAIC_c removed from the best performing model ($w_i = 0$).

Table 2. Summary of GLMM with year of shark discovery as the response variable with Total length, Latitudinal range, Depth range, Mid-point of the depth range, and Trophic level as fixed effects, and Shark Genus:Family:Order as the random effect. Predictor variable relative importance weights [w + (*i*)], ranks, weighted model average parameter estimates, and 95% confidence intervals. Estimates for fixed effects in bold indicate those with a 95% confidence interval bounded away from ‘0’.

Random effect	Group		Variance (%)	
n = 96	Shark Genus: Family:Order		16.08	
Fixed effects Predictor variable	w + (*i*)	Rank	Parameter estimate	95% CI
Total length	**1.00**	**1**	**−50.73**	**−69.29 to −32.17**
Latitudinal range	**1.00**	**1**	**−56.54**	**−65.68 to −47.41**
Depth range	0.83	5	−2.33	−11.26 to 5.61
Mid. of depth range	**1.00**	**1**	**16.67**	**6.35 to 27.10**
Trophic level	**0.99**	**4**	**21.48**	**4.02 to 39.25**

Discussion

Our findings suggest that the current discovery rate of new shark species is greater than at any other time in history and coincides with large rates of population decline. As such, further estimates of the global biodiversity of sharks using methods used herein, or other methods, would yield large confidence intervals associated with large margins of error due to the unpredictable variations associated with the species discovery process (Bebber et al. 2007). Hence, rather than make a futile attempt at estimating the number of species yet to be described, we place the emphasis on the surprising fact that sharks are being described at an unprecedented rate despite these animals being large-bodied and charismatic. Despite few recorded extirpation event (Ferretti et al. 2005, Luiz and Edwards 2011) and no documented shark extinction, deep-water sharks are especially vulnerable to extirpation. For instance, fishing related mortality of 38–58% of that estimated for oceanic or coastal species can drive them to extinction (Garcia et al. 2007). Thus, given current declines in sharks, extinctions/co-extinctions of many shark species are likely to occur prior to their formal discovery and description. Our results further indicate that smaller-bodied shark species are more prone to population declines, regardless of their latitudinal and depth range, whereas the rates of change are strongly structured by phylogeny.

Molecular tools and deep-sea fisheries are likely two main factors explaining the increase in species discovery rate since the mid-1980s. Molecular tools such as DNA barcoding have detected previously unrecognised cryptic species in diverse taxa (Hebert et al. 2004, Leung et al. 2009, LeGall and Saunders 2010). Since the popularising of DNA barcoding in 2003 (Hebert et al. 2003), 83 species of sharks have been described, of which 13 (or 15.7%) involved molecular/genetic tools (e.g. barcoding), including one scyliorhinid shark (Iglesias et al. 2004), three hemiscyllid sharks (Allen and Erdmann 2008, Allen and Dudgeon 2010), and nine squalid sharks (Last et al. 2007). Furthermore, molecular tools have uncovered a cryptic diversity within known species (Naylor et al. 2012), including among deep-water lantern sharks in the southern hemisphere (Straube et al. 2011) and coastal wobbegongs in Australia (Corrigan et al. 2008). A further high degree of cryptic diversity is suspected in deep-water sharks (Ward et al. 2005, 2007, Schaaf da Silva and Ebert 2006, White et al. 2008).

Coastal areas represent approximately 8.8% of the Earth’s surface whereas deep-sea habitats cover approximately 53% of the planet’s surface (Smith 2007) and remain relatively unexplored. With most fisheries fully or overexploited (Mora et al. 2009, Worm et al. 2009), fishing efforts have continued to shift from coastal to offshore/deeper waters

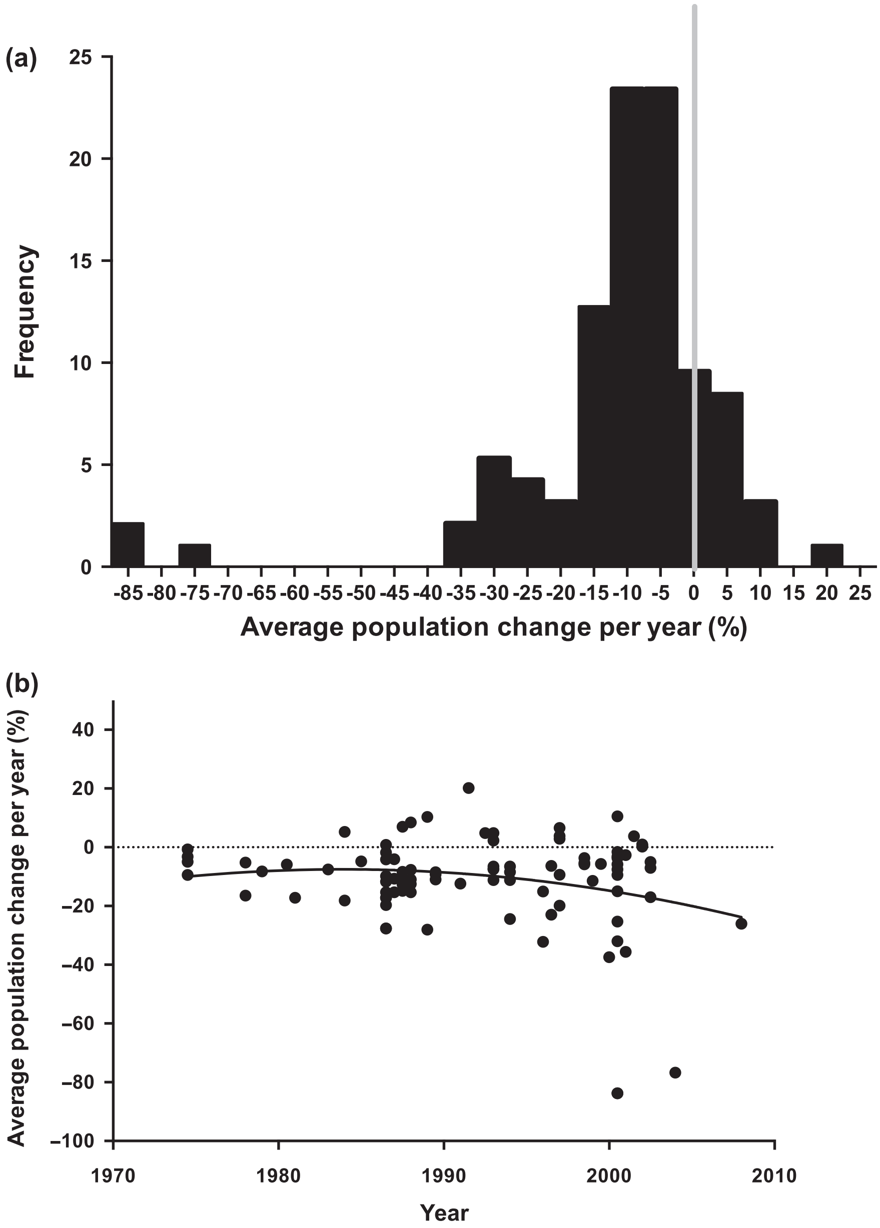

Figure 4. Contemporary (median year > 1970) average annual rates of population decline in sharks: (a) frequency distribution (grey line represents 'no change') and (b) relationship with median year during which there was an observed change in abundance. The best line in (b) represents the best-fit relationship from a non-linear regression (quadratic equation; $p = 0.0117$; $r = 0.22$).

(Roberts 2002, Morato et al. 2006, Swartz et al. 2010), thereby increasing encounter opportunities with new shark species. Hence, the mid-point of the depth range of sharks has become a proxy for accessibility. Furthermore, as fisheries now exploit depths surpassing the maxima recorded for sharks, there are no depth refugia remaining (Priede et al. 2006). Nevertheless, several shallow water shark species have been described in the past five years (Supplementary material Appendix 1). For instance, three species described in 2008 inhabit shallow coastal waters at depth < 20 m: *Hemiscyllium galei*, *Orectolobus reticulatus*, and *Glyphis garricki*. Interestingly, the latter is also a large-bodied species reaching a maximum total length of over 250 cm.

Another pattern of some marine fisheries is a shift from higher to lower trophic levels of target species, i.e. fishing down the food chain (Pauly et al. 1998, 2000), although this is not without exception (Essington et al. 2006, Branch et al. 2010, Wilen and Wilen 2012). In marine ecosystems, despite body size being a weak predictor of trophic level at the species level (Jennings et al. 2001), larger individuals in a community feed at a higher trophic level (Sheldon et al. 1972, Randhawa and Brickle 2011). Consequently, larger-bodied sharks were likely encountered earlier than smaller sharks occupying lower trophic levels, consistent with our result that body size is a predictor of year of discovery. Fishing down the food chain (Pauly et al. 1998, 2000) has also been reported as one of the causes of declines of large predatory sharks (Myers and Worm 2003). However, our results did not reveal trophic level to be a predictor of the rate of shark population decline. This is akin to Pinsky et al. (2011)

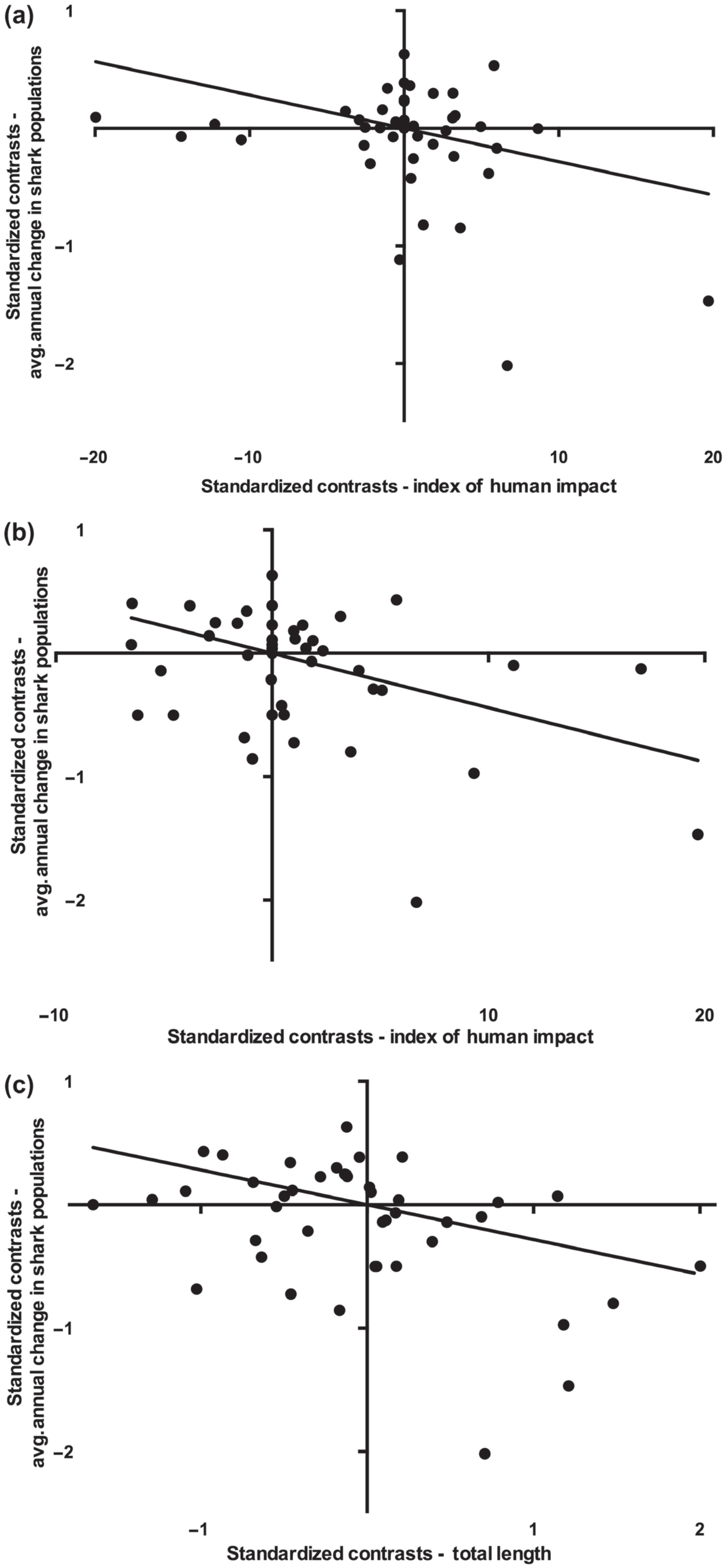

Figure 5. Relationship between the standardized contrasts of the average annual rate of change in shark populations (*r*) and (a) standardized contrasts for index of human impact (least extreme *r*-values per species), (b) standardized contrasts for index of human impact (most extreme *r*-values per species) and (c) standardized contrasts for shark total length (most extreme *r*-values per species).

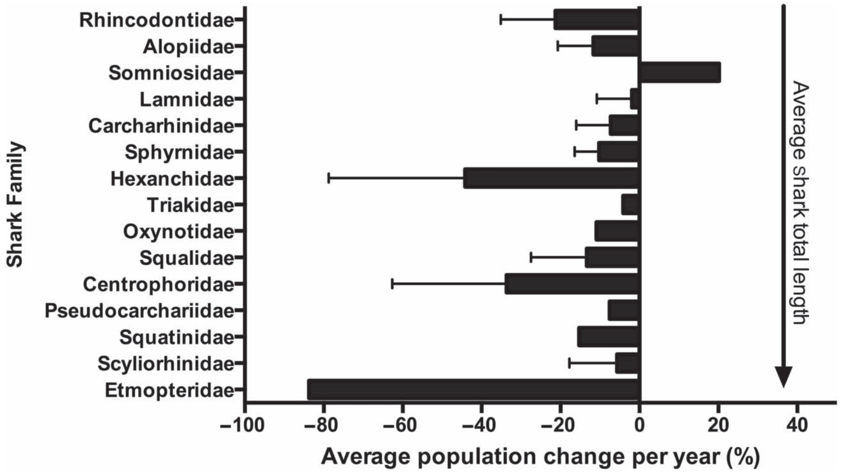

Figure 6. Average annual rate of change in shark populations per shark Family. Error bars represent a single standard deviation. Where no error bar is present, the shark Family is represented by a single species in our analyses. All shark families have been placed on this graph in order of increasing total length (averages calculated from taxa represented in our analyses only), with the smallest average total length at the bottom of the graph and the family with the largest average total length at the top (see arrow).

who found no evidence for evolutionary (phylogenetic) influences or life history traits, including trophic level, as strong predictors of fisheries collapse.

It should be noted here that, although unlikely to affect our conclusions, the subset of species for which data on changes in abundance were available are not a random subset of all shark species: comparison of our samples with the overall shark database on Fishbase using t-tests for unequal variance suggests that the species included in our analyses show a bias towards larger sharks (366.2 ± 381.3 vs 122.5 ± 151.2 cm; $t = 7.685_{518}$, $p < 0.0001$) occupying higher trophic levels (4.155 ± 0.379 vs 4.017 ± 0.294; $t = 2.477_{504}$, $p = 0.0136$). Contrary to Essington et al. (2006) and Fisher et al. (2010) who both reported that the decline of large-bodied and high trophic level marine species is a phenomenon restricted to the North Atlantic, our analyses, including geographical Locality as a random effect, revealed no locality bias. However, our results may differ due to the focus on sharks which, due to their life histories, are generally prone to decline more so than other marine species (Musick et al. 2000, Stevens et al. 2000, Frisk et al. 2001, Myers and Worm 2005).

Body size has been linked to extinction risk in chondrichthyans (Field et al. 2009), although the relative importance of this variable is attenuated significantly when considering effects of shared ancestry on extinction risk (Field et al. 2009) or average rate of change in population abundance (herein). However, surprisingly, our results suggest that smaller sharks are more prone to population declines than larger-bodied relatives (Table 3 and Fig. 6). Here, it is important to consider the combined proportion of the variance explained by random effects (shark species nested within Genus:Family:Order and Geographical locality) on average annual change in population abundance (78%), leaving a small proportion of the variance explained by fixed effects and a weak pattern of greater rates of decline in smaller shark species once phylogeny is taken into account, only when the most extreme declines for each species are considered (Fig. 5c). Many of the smaller sharks represent mesopredators and despite mesopredatory shark release being a common consequence of removing apex predators (Myers et al. 2007), a reversal can occur within a decade (Myers and Worm 2003) due to populations of mesopredators increasing to levels exceeding the carrying capacity of the ecosystem. Many of the studies from which information was extracted herein have been recent, hence declines observed for smaller sharks may be more recent than those for apex predators (some dating back to the 19th century – Supplementary material Appendix 2), translating into more abrupt changes due to the shorter time period accounted for in our calculations.

Human impacts in marine ecosystems are not limited to fishing related activities. These include also pollution, variations in ocean chemistry due to climate change, and the introduction of species to new ecosystems (Halpern et al. 2008). As such, it is predicted that organisms facing

Table 3. Summary of GLMM with average rate of population change as the response variable with Total length, Latitudinal range, Depth range, Mid-point of the depth range, Trophic level, and index of Human impact as fixed effects, and Shark Species:Genus:Family:Order (S:G:F:O) and Geographical locality as random effects. Predictor variable relative importance weights [w + (*i*)], ranks, weighted model average parameter estimates, and 95% confidence intervals. Estimates for fixed effects in bold indicate those with a 95% confidence interval bounded away from '0'.

Random effect	Group		Variance (%)	
n = 45	Shark S:G:F:O		74.72	
n = 9	Geographical locality		3.13	
Fixed effects				
Predictor variable	w + (*i*)	Rank	Parameter estimate	95% confidence interval
Total length	0.88	4	−1.04	−20.11 to 17.74
Latitudinal range	0.91	3	−7.05	−31.27 to 15.84
Depth range	0.94	2	−11.88	−31.21 to 5.88
Mid. depth range	0.85	5	−2.92	−17.24 to 10.39
Trophic level	0.96	1	16.04	−3.42 to 36.76
Human impact	0.63	6	−0.94	−3.28 to 0.29

higher levels of human disturbance will be negatively impacted. Although our study found weak evidence linking shark population declines to human impacts, the trend revealed by PIC analyses is one of lower average annual rates of decline with increasing human impact. Furthermore, most regions from which shark population data were extracted are only moderately impacted by human activities (Supplementary material Appendix 4) with the majority of localities falling in the medium to medium-high impacted regions (Supplementary material in Halpern et al. 2008). However, our analyses did reveal an influence of geographical locality on observed declines, where human impact may represent a confounding variable imbedded within locality acting synergistically. Only if more precise information on geographical localities contributing to individual studies used to compile our dataset were to become available could we tackle this issue.

The high rate of decline in sharks may be a product of their life histories and sensitivity to even the lowest of fishing pressures likened to those of artisanal and subsistence fishing (Ferretti et al. 2010). Additionally, their continued decline, despite conservation efforts, may have to do with range contraction or an Allee effect. Although neither has been documented in sharks, range contractions ranging between two to 46% have been observed in nine of 13 tuna and billfish species studied globally between 1960 and 2000 (Worm and Tittensor 2011). Furthermore, population declines exceeding 99% in large predatory sharks (Supplementary material Appendix 2 and references therein) with poor recovery potential could very well maintain low population sizes due to Allee effects, although we were not able to test for this in our analyses.

Sharks play important roles in marine communities (Bascompte et al. 2005, Myers et al. 2007), but increasing anthropogenic stress is depleting populations at alarming rates (Fig. 4 and Supplementary material Appendix 2 and references therein). For instance, in the tropical Pacific, the combined effects of a reduction in size and abundance in large predators caused by fishing has led to a 10-fold decrease in the biomass of this functional group (Ward and Myers 2005). Consequently, the removal of large predatory sharks can lead to trophic cascades defined by disruption in top-down control (Stevens et al. 2000, Shepherd and Myers 2005, Ferretti et al. 2008, 2010, Baum and Worm 2009, Barnett et al. 2012) and a reduction in overall omnivory (Bascompte et al. 2005). Furthermore, large predatory sharks can increase connectivity between habitats/ecosystems (McCauley et al. 2012). However, consequences of perturbations on food webs, caused by the removal of top-predatory or meso-predatory sharks, although likely severe, cannot be assessed adequately. We are hindered by an inability to extrapolate the robustness of communities involving sharks due to the lack of knowledge about the connectedness in these food webs. Therefore, not only are conservation efforts necessary to maintain stability in these communities, but also to prevent local extirpation or extinction of both described and yet to be described shark species.

Acknowledgements – Comments and suggestions by C. Duffy, L.-R. Arteau, and members of the Evolutionary and Ecological Parasitology Research Group at Otago contributed to vastly improving an earlier version of this manuscript. We are grateful to the Univ. of Otago for financial support.

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Supplementary material (Appendix ECOG-00793 at <www.ecography.org/readers/appendix>). Appendix 1–5.