Ambio
DOI 10.1007/s13280-015-0683-3

REPORT

Estimating biodiversity impacts without field surveys: A case study in northern Borneo

Justin Kitzes, Rebekah Shirley

Received: 20 March 2015 / Revised: 14 June 2015 / Accepted: 18 June 2015

Abstract In many regions of the world, biodiversity surveys are not routinely conducted prior to activities that lead to land conversion, such as development projects. Here we use top-down methods based on global range maps and bottom-up methods based on macroecological scaling laws to illuminate the otherwise hidden biodiversity impacts of three large hydroelectric dams in the state of Sarawak in northern Borneo. Our retrospective impact assessment finds that the three reservoirs inundate habitat for 331 species of birds (3 million individuals) and 164 species of mammals (110 million individuals). A minimum of 2100 species of trees (900 million individuals) and 17 700 species of arthropods (34 billion individuals) are estimated to be affected by the dams. No extinctions of bird, mammal, or tree species are expected due to habitat loss following reservoir inundation, while 4–7 arthropod species extinctions are predicted. These assessment methods are applicable to any data-limited system undergoing land-use change.

Keywords Impact assessment · Population · Abundance · Land use · Landscape

INTRODUCTION

Driven by increasing human population and consumption demands, global land use change continues at a rapid pace. Despite the widely acknowledged relationship between habitat loss and biodiversity loss (Millennium Ecosystem Assessment 2005), there are often no biodiversity surveys conducted prior to land conversion. Without baseline data, the impacts of habitat loss often remain uncertain and largely hidden from the public. Information on these impacts, however, is critical to understanding the scope of global biodiversity loss, targeting lands for protection, and balancing tradeoffs between environmental concerns and development objectives.

In the absence of direct empirical data, two broad classes of approaches, top-down and bottom-up, can be used to provide information on the potential biodiversity impacts associated with habitat loss. The first approach relies on large-scale maps of species occurrences, generated via expert assessment, atlas data, or species distribution models. Occurrence maps, such as those produced by the International Union for Conservation of Nature (IUCN) Redlist and Birdlife International, can be used directly to estimate the number and identity of species whose ranges overlap with a location of habitat loss (e.g., Finer et al. 2008; Kitzes 2012) or used as an input into algorithms that support managers and policy makers in evaluating the biodiversity loss associated with different planning scenarios (Sarkar et al. 2006; Ball et al. 2009). These maps, however, are only available for well-studied taxa, such as birds and mammals, and do not generally provide information on the impacts of habitat loss on species populations.

In contrast, the bottom-up approach relies on the availability of high quality small-scale data, such as complete censuses of all of the species in a small plot, that is "upscaled" using statistical or theoretical scaling relationships. For example, the species–area relationship (SAR), which can be used to estimate changes in species richness with changes in area, is frequently used for estimating potential diversity and extinction rates in uncensused areas (May et al. 1995). These applications of the SAR, however, are less straightforward than commonly assumed, as complexities such as

Electronic supplementary material The online version of this article (doi:10.1007/s13280-015-0683-3) contains supplementary material, which is available to authorized users.

Published online: 14 July 2015

the appropriate functional form of the relationship, habitat geometry, complex patterns of habitat loss, and species overlap between multiple patches must be carefully considered (Ney-Nifle and Mangel 2000; Koh et al. 2010; He and Hubbell 2011; Koh and Ghazoul 2010). Additionally, the most widely used equation for the SAR, a power law, has come under increasing criticism from several empirical and theoretical angles (Dengler 2009; McGlinn et al. 2013), and more recently developed and better tested scaling theories have not yet been integrated into applied ecology.

In this research, we use both top-down and bottom-up methods to estimate the biodiversity impacts associated with habitat loss following the creation of three large hydroelectric dams in the state of Sarawak in northern Borneo. Our approach goes beyond simple species counts to estimate three distinct measures of biodiversity impact for each dam and all three dams together: the number of affected species, number of local extinctions, and number of lost individual organisms. The number of lost individuals is important both directly as a measure of decreased species abundances as well as indirectly as a proxy for the number of lost demographic or genetically distinct populations within species (Ehrlich and Daily 1993; Hughes et al. 1997). These estimates are completed for four taxonomic groups, mammals, birds, trees, and arthropods, with top-down methods applied to the relatively well-studied mammals and birds and bottom-up methods applied to trees and arthropods. While the predictions from these models are necessarily uncertain, this approach provides the best available means of estimating biodiversity impacts when field surveys prior to habitat loss are not available.

MATERIALS AND METHODS

Study site

The rapid economic growth sustained in Southeast Asia throughout the new millennium has led to a surge in large-scale infrastructure projects to facilitate industrial productivity and consumption (IEA 2013; OECD 2013). The "mega-dam" in particular has returned to public planning policy as a solution to increasing energy demand in the region, with many new dams currently under construction across Laos, Thailand, and Cambodia (Goh 2007). This trend extends to Malaysia, one of the fastest growing economies in Southeast Asia, where part of the federal government near-term economic growth strategy (the Tenth Malaysia Plan) involves building at least 12 mega-dams in the state of Sarawak to attract energy-intensive industry and stimulate local production (Keong 2005; Sovacool and Bulan 2011).

The state of Sarawak, located along the northern coast of the island of Borneo (Fig. 1), is the poorest and most rural state in Malaysia. This area has long been a focal point for the development of large-scale hydroelectric power given its characteristically heavy rainfall and elevated topography. At least six dams are scheduled to be completed in Sarawak by 2020, with three major dams already under different stages of development (Sovacool and Bulan 2012a). In 2012, the 2400 MW Bakun dam became operational, and as of 2014, the reservoir for the 944 MW Murum dam is being filled. Access roads for the 1200 MW Baram dam have been cleared, although preparatory construction work has remained stalled since 2013 due to road blockades and protests from local NGOs (Lee et al. 2014).

In addition to displacing 30 000–50 000 indigenous people, the development of the 12 mega-dams would result in at least 2425 km^2 of direct forest cover loss (Bruno Manser Fund 2012). The three initial dams discussed above, whose reservoirs will together flood an expected total area of 1354 km^2 (700 km^2 for Baram, 242 km^2 for Murum, 413 km^2 for Bakun), are the focus of our analysis.

The island of Borneo, part of the Sundaland biodiversity hotspot (Myers et al. 2000), is notable both for its high levels of biodiversity and highly threatened natural ecosystems (Sodhi et al. 2010; Koh et al. 2013). Borneo's forests house the highest level of plant and mammal species richness in Southeast Asia (Bellard et al. 2014), including 581 species of birds and 240 species of mammals, and the island is considered a major evolutionary hotspot (de Bruyn et al. 2014). Extensive development has led to significant land cover change on the island, with 389 566 km^2, approximately 53 % of the total area of the island, remaining under natural forest cover (Gaveau et al. 2014).

Birds and mammals

Species affected

To estimate the number of species affected by dam construction, global range maps for birds were requested from Birdlife International (Birdlife International 2011) and global range maps for mammals were obtained from the IUCN (IUCN 2011). For both birds and mammals, species ranges were filtered to include only those with Presence code 1 or 2 (Extant and Probably Extant), Origin code 1 (Native), and Seasonal code 1 (Resident). These range maps were clipped with polygons representing the expected reservoir inundation areas for the three dams, obtained from the Sarawak Geoportal published by Bruno Manser Fonds (Bruno Manser Fonds 2014), and the species found within each reservoir area were identified and counted.

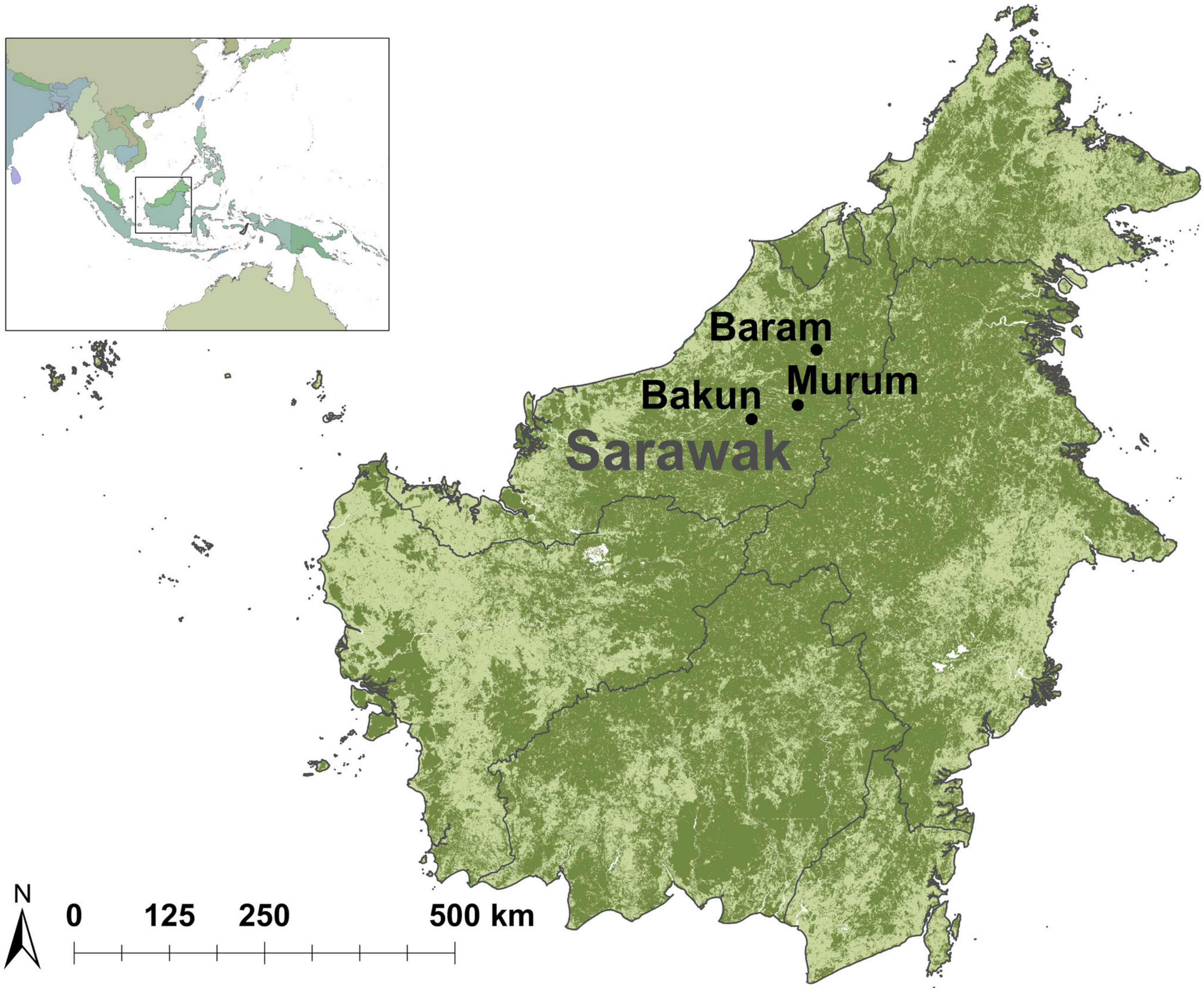

Fig. 1 Location of Bakun, Murum, and Baram dams in northern Borneo. *Dark green* shows forest cover (ESA GlobCover 2009 Global Land Cover Map) and *light green* other terrestrial land cover types

Extinctions

The number of determined extinctions due to reservoir inundation was calculated conservatively as the number of species whose ranges are completely overlapped by the reservoir areas. As a fractional loss of range may still contribute to extinction risk for individual species (e.g., Thomas et al. 2004; Kitzes and Harte 2014), however, these fractions were also examined for all affected bird and mammal species.

Individuals lost

For birds, a central estimate of the total number of lost individuals across all species was estimated by multiplying reservoir areas for each dam by an estimated typical bird density of 2500 individuals per km^2 (Gaston et al. 2003) for tropical forest. For mammals, the number of individuals lost for each species was estimated by multiplying the area of a species' range intersecting the reservoir area by an observed or estimated population density for that species. Where available, empirical densities were drawn from the PanTHERIA database (Jones et al. 2009). Where empirical density was not recorded in PanTHERIA but adult body mass was available, population density was estimated from a log–log linear regression of body size on empirical population density for those species with both density and body size data in the PanTHERIA data set (Supplementary Material). We note that while specific individuals present in the reservoir area during inundation may be able to migrate to avoid immediate death, the long-term abundance of both groups is presumed to be proportional to resource availability and hence habitat area. Any migrating individuals are thus not expected to permanently increase population densities surrounding the reservoirs.

Trees and arthropods

For trees and arthropods, range maps and atlas data are not generally available for individual species. Our estimates of impacts for these groups are thus based on bottom-up macroecological scaling laws and census data from comparable landscapes outside of the dam region.

Two macroecological scaling laws are used below: the SAR, which gives the expected number of species found in a habitat patch as a function of area, and the endemics–area relationship (EAR), which gives the expected number of species within a large reference region that are found only within a smaller habitat patch of a certain area (i.e., the number of species that are locally endemic, with respect to the larger region, to the small patch). Of the many functional forms that have been proposed for these metrics, we here use the equations derived from a particularly successful maximum entropy theory of ecology (Harte et al. 2008; Harte 2011).

Census data

For trees, many complete censuses of forest plots are available throughout the world through the Center for Tropical Forest Science network (Losos and Leigh Jr. 2004). The closest censused plot to the dam region is the Lambir Hills Forest Dynamics Plot, a 52 ha mixed dipterocarp forest plot in northern Borneo, which contains 1174 species and 366 121 individual trees >1 cm diameter breast height (Condit et al. 2000). This plot, however, is noted for its unusually high species richness due to an abrupt soil gradient that occurs within the plot, and as such the richness observed here may be larger than the expected richness at this area across the entire forested region of northern Borneo. A 50 ha plot of lowland diterocarp forest at the Pasoh Forest Reserve in Peninsular Malaysia, for comparison, contains 818 species across 320 382 individuals (Condit et al. 2000). For subsequent analysis, we take the Lambir plot to represent an upper estimate of richness and the Pasoh plot to represent a lower estimate, with the average of these two predictions at larger scales used as the central estimate.

Globally, there are very few equivalently complete arthropod censuses (Forister et al. 2014). For the bottom-up methods used in this analysis, an arthropod census must be taxonomically broad, use indiscriminate sampling methods designed to sample arthropods with different habitat preferences, and be drawn from a complete and clearly defined contiguous area. Of the arthropod censuses conducted in Borneo (Kitching et al. 2001; Basset et al. 2003; Beck et al. 2006; Dial et al. 2006; Beck and Rüdlinger 2014; Stork 2015, and references therein), we are not aware of any that meet these three criteria. The most comprehensive census of which we are aware that meets these criteria is a survey of lowland tropical forest in the San Lorenzo forest, Panama (Basset et al. 2012). Although there are many abiotic, structural, and taxonomic differences between this Panamanian forest and the study area of northern Borneo, we believe that this very comprehensive data set is less prone to bias in biodiversity estimation than more limited studies conducted in southeast Asia. To the extent that the tropical forests of Borneo are richer in tree species, for example, than similar forests in central America, the arthropod impacts given here may be low-end estimates.

Basset et al. (2012) sampled a total of 12 plots, each 0.04 ha in area, using a variety of census methods, not all of which were applied at all plots. For subsequent estimates, we use data from eight of these plots, excluding data from four that display undercounting of relatively abundant insect orders (Harte and Kitzes 2015). Calculations were completed using data from all eight plots, with minimum, maximum, and mean predictions based on individual plots representing our lower, upper, and central estimated species richness at large scales.

Species affected

The number of tree and arthropod species affected by reservoir inundation was estimated using a SAR. The most commonly applied form of the SAR is a power law, $S = cA^z$, where c is a fitted intercept, A is habitat area, and z is a constant slope often taken to be near 0.25. While this power law SAR has a long history of application in ecology and conservation, ecosystems show substantial variation around this slope (Rosenzweig 1995; Drakare et al. 2006), and it was recently recognized that empirical SARs show systematic decreases in log–log slope with the mean number of individuals per species at any spatial scale (Harte et al. 2009; Wilber et al. 2015). This pattern suggests that traditional SAR applications that use a log–log slope of 0.25 to upscale small-scale census data will almost certainly overestimate large-scale species richness.

The number of species affected by reservoir inundation was estimated using a SAR predicted by the maximum entropy theory of ecology of Harte et al. (2008), which closely fits the empirical pattern of decreasing SAR slope at large scales (Harte et al. 2009). The iterative variant of this curve (Harte 2011; McGlinn et al. 2013), which has successfully upscaled tree richness and has been applied to upscaling arthropod richness (Harte and Kitzes 2015), was used here. This SAR is recursively calculated at successively larger doublings of area by solving the coupled equations

$$S(2A) = S(A)x + N(2A)x\left(\frac{1-x}{x - x^{N(2A)+1}}\right) \times \left(1 - \frac{x^{N(2A)}}{N(2A)+1}\right) \quad (1)$$

and

$$S(2A) = N(2A)x^{N(2A)}(-\phi(x, 1, N(2A)+1) - \ln(1-x)) \times \left(\frac{x-1}{x(x^{N(2A)}-1)}\right) \quad (2)$$

for $S(2A)$, where $S(A)$ and $N(A)$ are the known number of species and individuals at area A and $S(2A)$ and $N(2A)$ are the number of species and individuals at twice area A (Supplementary Material). The parameter x is an unknown constant, and $\phi(n)$ is the Lerch phi function. For large areas A' falling between exact doublings of area A, S', the number of species in A', can be interpolated linearly on a log–log scale. A Python function to perform these calculations is included in Supplementary Material, and pre-calculated results for a range of parameters are included in Table S1 (see also Fig. S1).

An important shortcoming of the SAR is that it applies only to a single contiguous habitat area and thus cannot directly estimate the total number of species found across all three reservoir areas combined. In the absence of information on overlap, the total number of species affected across the three reservoirs can still be bounded (Kinzig and Harte 2000). A low estimate presumes that the species lists across reservoirs are completely nested, such that the number of species affected by the single reservoir with the highest low-end estimate of richness is equal to the total number of species affected across all three reservoirs, while a high estimate can be generated as the upper estimate of the number of species that would be affected by a single patch with an area equal to the combined areas of the three reservoirs.

Extinctions

The number of extinctions associated with the inundation of the three reservoirs can be estimated through a second application of the SAR in concert with an EAR, which estimates the expected number of species within a large region that are found only in a habitat patch of a certain area (Harte and Kinzig 1997). In contrast to the case of birds and mammals, where global range maps allow for the measurement of global extinctions, the EAR can be used only to estimate extinctions with regard to a surrounding reference bioregion. For this analysis, the reference region is considered to be the remaining tropical forest on the island of Borneo, and our extinction estimates for trees and arthropods thus refer to extirpations of forest-dwelling species from the island. To the extent that tree and arthropod species found on Borneo are found only on the island and not elsewhere, these local extinctions will also correspond to global extinctions.

The maximum entropy theory described above also predicts a complementary EAR (Harte 2011), which, when the area lost is small relative to the large region, can be approximated by the linear relationship

$$E = -\frac{S^*}{\ln(1-p)}\left(\frac{A'}{A^*}\right), \quad (3)$$

where S^* is the number of species in the reference region, A^* is the area of that region, and A' is the reservoir area. The parameter p is calculated by solving the implicit equation

$$\frac{N^*}{S^*} = -\frac{1}{\ln(1-p)}\frac{p}{(1-p)}, \quad (4)$$

where N^* is the number of individuals in the reference region. As the value of S^* is unknown, it is estimated as the central estimate of the SAR procedure described above with $A^* = 389\,566$ km^2, the remaining forested area of Borneo. The value of N^* is similarly unknown, and is estimated by linearly scaling the measured number of individuals in the small plots N, to the area A^* (see also below). If A' were not small relative to A^*, a numerical evaluation of the exact EAR equation would be needed in place of the above approximation (Harte 2011).

As in the case of the SAR, the EAR alone is not sufficient to estimate the total number of local extinctions across all three reservoirs, as this metric does not consider overlap in species lists between reservoir areas (Kinzig and Harte 2000). A low bound on the total number of local extinctions is the sum of the lower EAR estimates from the three areas, as this gives the count of species locally endemic to one of the three reservoirs. This sum ignores, however, species that are locally endemic to two or more of the reservoir areas, which would not be lost if a single reservoir was flooded but will be lost when the set of three reservoirs are created. Similar to the SAR, an upper bound on local extinctions can be estimated as the upper result from applying the EAR to a hypothetical single plot with area equal to the sum of the three reservoir areas.

Individuals lost

To calculate the number of individual trees or arthropods lost due to reservoir inundation, the density of individuals in small plots is scaled linearly to the reservoir areas as $N' = N(A'/A)$, where N' is the number of individuals at the reservoir area A'. This calculation presumes that the measured density in the small plot is representative of the density of all individuals, across species, in the larger region. As there are no issues of overlap associated with estimates of lost individuals, lower and upper estimates for the three reservoirs together are calculated as the sum of the lower and upper estimates for all reservoirs, respectively.

RESULTS

Top-down global range maps show that the reservoir areas overlap habitat for a total of 331 species of birds and 164 species of mammals (Tables 1, S2; Fig. 2). For both taxa, there is substantial overlap in the species affected by individual dams, with the Baram dam alone affecting 318 out of these 331 bird species and 162 out of these 164 mammal species. With regard to extinctions, no species of birds or mammals had its entire range contained within the reservoir inundation areas. Additionally, no birds or mammals were found to have more than 5 % of their total range located within the reservoir inundation areas (Table S2), which can be presumed to represent a negligible contribution to expected extinction risk. For comparison, the IUCN Red List v3.1 requires a species to experience a minimum population reduction of 30 % to be listed as Vulnerable, the least at-risk status of the three threatened categories. Using observed and estimated population density data, the three dams together are estimated to cause the loss of 3.4 million individual birds and 110 million individual mammals (Table 2).

Of the 331 bird species affected by the dams, two are categorized as endangered by the IUCN (*Ciconia stormi*, Storm's stork, and *Polyplectron schleiermacheri*, the Bornean peacock-pheasant) and 14 are considered vulnerable. One mammal species found in the dam region is classified as critically endangered (*Manis javanica*, the Sunda Pangolin), six species are considered endangered, and 24 are vulnerable (Supplementary Material). These endangered mammals are the endemic Bornean Bay Cat (*Catopuma badia*), the Sunda Otter Civet (*Cynogale bennettii*), the Grey Gibbon (*Hylobates muelleri*), the Hairy nosed Otter (*Lutra sumatrana*), the Flat-headed Cat (*Prionailurus planiceps*), and the Smoky Flying Squirrel (*Pteromyscus pulverulentus*).

Bottom-up estimates based on the SAR suggest that the three dam areas will affect 2100–3300 species of trees and 17 700–31 800 species of arthropods (Table 2). The combination of SAR and EAR methods suggest that there are likely to be few extinctions of tree or arthropod species due to dam inundation. Less than one extinction is expected for tree species, and arthropod extinctions are estimated from 4 to 7 species for all three dams combined (Table 2). Based on population density data from intensive census plots, an estimated 870–950 million individual trees and 34–73 billion individual arthropods (Table 2) will be lost due to reservoir inundation.

DISCUSSION

This analysis demonstrates that the Bakun, Murum, and Baram dams impose a potentially significant impact on the biodiversity of Borneo. While the results show that few or no species extinctions are expected for birds, mammals, trees, and arthropods, many species in all four taxa are expected to experience decreases in abundance due to habitat loss. Although the reservoir areas of these dams represent only 0.2 % of the total land area of Borneo, the 331 species of birds affected by the dams represent 57 % of the 581 species of birds found on the island of Borneo, and the 164 species of affected mammals represent 68 % of the 240 species on the island. The lower estimate of 2100 affected tree species similarly represents approximately two-thirds of the estimated 3000 species of trees on the island (Whitmore and Tantra 1987). The extent of these population losses ranges from the millions to the billions of individual organisms, depending on the taxa.

There are several important sources of uncertainty in our analysis, the majority of which suggest that the results above are likely a low-end estimate of the true biodiversity impacts of the dams. First, the application of the SAR and EAR do not account for the steeply sloping topography of the reservoir areas. Sloped areas such as these are likely to contain a greater diversity of abiotic conditions, which

Table 1 Estimates of the number of bird and mammal species affected and number of individual organisms lost due to habitat loss from reservoir inundation. No extinctions are expected for either of these taxa

Dam	Spp. affected		Individs. affected (millions)	
	Bird	Mamm	Bird	Mamm
Bakun	302	142	1.75	55.09
Murum	312	147	0.61	19.55
Baram	318	162	1.04	35.52
Total	331	164	3.4	110.16

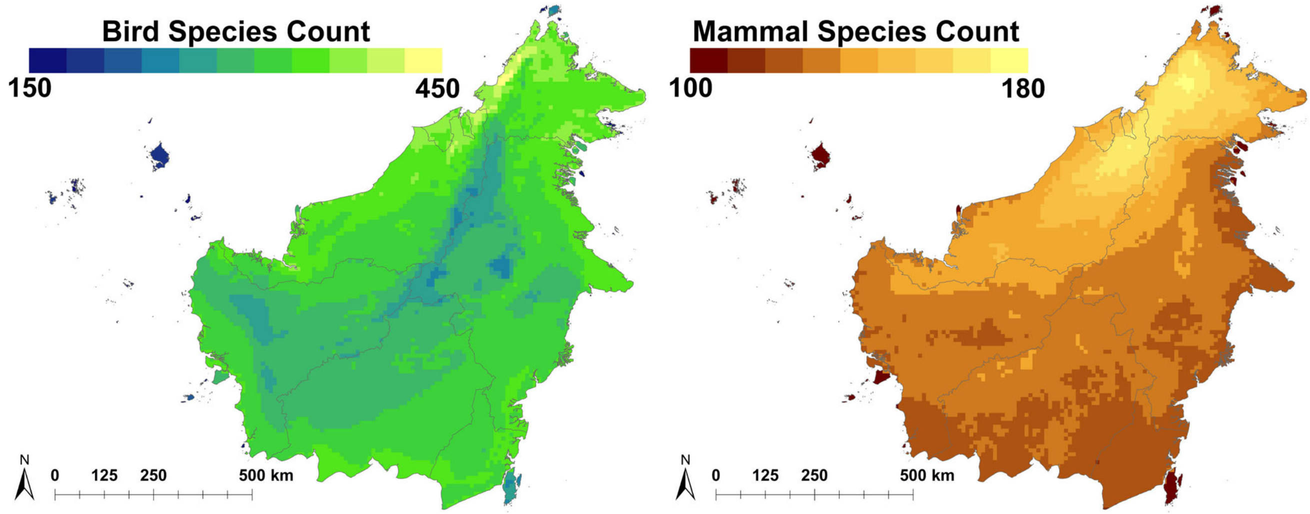

Fig. 2 Maps of bird and mammal species richness within Borneo, with dam locations

Table 2 Estimates of the number of tree and arthropod species affected, number of extinctions, and number of individual organisms lost due to habitat loss from reservoir inundation

Dam	Spp. affected (thousands)		Extinctions		Individs. affected (billions)	
	Tree	Arth	Tree	Arth	Tree	Arth
Bakun	2.62 (2.12–3.11)	24.49 (17.74–30.07)	0.38 (0.30–0.45)	3.08 (2.24–3.73)	0.47 (0.45–0.49)	25.83 (17.42–37.99)
Murum	2.35 (1.91–2.79)	22.25 (16.11–27.35)	0.13 (0.10–0.16)	1.06 (0.77–1.29)	0.16 (0.15–0.17)	8.92 (6.01–13.12)
Baram	2.48 (2.01–2.95)	23.37 (16.93–28.71)	0.22 (0.18–0.27)	1.82 (1.32–2.20)	0.28 (0.26–0.29)	15.22 (10.26–22.38)
Total	2.12–3.31	17.74–31.80	0.58–0.88	4.34–7.22	0.87–0.95	33.69–73.49

would lead to steeper than average slopes for the SAR and EAR and hence higher numbers of affected species and extinctions than predicted above.

Second, the estimates of species-level extinctions do not reflect potential extinctions of subspecies or local populations, both of which may be critical to species' long-term viability (Ehrlich and Daily 1993; Ceballos and Ehrlich 2002). Our measure of the number of lost individuals within taxonomic groups is thus an important complement to extinction analyses, as it has been suggested that the loss of genetically or demographically distinct populations may scale linearly with area and hence the loss of individuals (Hughes et al. 1997).

Third, the estimates of the number of lost individuals rely on expected population density estimates derived from global data sets, in the case of mammals and birds, or small-plot censuses, in the case of trees and arthropods. In both cases, the reservoir-scale estimates of individuals lost can be interpreted as the best estimate of the statistical expectation of decreases in abundance, given the available data. Thus, while variability in these densities across space will lead to additional uncertainty around the predicted decreases in abundance, we do not expect that the central estimates themselves will be biased due to spatial variation in abundance.

Fourth, the estimates of the number of bird and mammal species affected by the dams, and the associated number of affected mammal individuals, may be an overestimate, as species ranges contain "holes" across spatial scales that are not reflected at the level of the global range maps. The number of affected species in these taxa should thus be understood as the number with the potential to use the habitat inundated by the reservoir areas, not necessarily the number that were inhabiting the area at the moment of inundation.

Fifth, this analysis does not account for the many impacts of these three dams on biodiversity that are not directly related to habitat loss from reservoir inundation. A full accounting of the dam impacts would need additionally to include the roads and other infrastructure related to dam construction and operation, downstream changes to the river and flooding regime and their affect on habitat, impacts on river species, and indirect costs stemming from displaced communities, economic activity outside the dam region, and greenhouse gas emissions from the reservoirs.

Finally, although outside of the scope of this analysis, we note that climate change and habitat loss are likely to have synergistic future impacts on biodiversity that are not addressed here. Borneo is projected to experience annual maximum temperature increases above the global average and increased precipitation variability under a 2 °C temperature increase (Johnson 2012). One recent study finds that as many as 49 % of mammalian species in Borneo will lose more than a third of their habitat by 2080 when climate and deforestation impacts are considered together, a twofold increase over historical trends (Struebig et al. 2015). With suitable ecological conditions predicted to shift upslope for many of these species, preserving upland forest areas, such as those inundated by the three reservoirs examined in this analysis, takes on additional significance.

CONCLUSION

The approach presented here provides a simple and scalable method for assessing landscape-scale diversity in a manner that can be relevant for policy and management. In the case of the Sarawak hydroelectric dams, a state and national level debate on the suitability of the dams continues to unfold, involving affected village communities, subsistence farming populations, commercial plantation interests, timber interests, land-rights advocacy groups, conservationists, utility companies, forest management authorities, state development planners, and other stakeholders (Sovacool and Bulan 2011, 2012b). Regardless of the weight or priority that different stakeholders give to biodiversity, the ability to rapidly consider the risks posed to species and populations under alternative scenarios will allow for more informed opinions and discussions of tradeoffs.

In the absence of field surveys prior to the construction of three hydroelectric dams in northern Borneo, this analysis has provided a quantitative means of retrospectively assessing the biodiversity impacts of these projects. While few species-level extinctions are expected, the results show that a significant fraction of the resident species of Borneo are likely to suffer reduced populations due to habitat loss following reservoir inundation. More broadly, the methods presented here provide a readily applicable tool for estimating biodiversity impacts under alternative development scenarios when few empirical data are available. Given the rapidity of land conversion and biodiversity loss in many regions of the world, model-driven approaches such as these will be critical for illuminating the otherwise hidden biodiversity costs associated with global land-use change.

Acknowledgments We thank D. Kamman, J. Harte, and M. Potts for helpful comments on drafts of this manuscript. This work was supported in part by an Advancing Theory in Biology award from the National Science Foundation.

REFERENCES

Ball, I., H. Possingham, and M. Watts. 2009. Marxan and relatives: Software for spatial conservation prioritisation. In *Spatial conservation prioritisation: Quantitative methods and computational tools*, ed. A. Moilanen, K. Wilson, and H. Possingham, 185–195. Oxford: Oxford University Press.

Basset, Y., R. Kitching, S. Miller, and V. Novotny, eds. 2003. *Arthropods of tropical forests: Spatio-temporal dynamics and resource use in the canopy*. Cambridge: Cambridge University Press.

Basset, Y., L. Cizek, P. Cuénoud, R.K. Didham, F. Guilhaumon, O. Missa, V. Novotny, F. Ødegaard, et al. 2012. Arthropod diversity in a tropical forest. *Science* 338: 1481–1484.

Beck, J., and C.M. Rüdlinger. 2014. Currently available data on Borneo geometrid moths do not provide evidence for a Pleistocene rainforest refugium. *Raffles Bulletin of Zoology* 62: 822–830.

Beck, J.A.N., I.A.N.J. Kitching, and K.E. Linsenmair. 2006. Effects of habitat disturbance can be subtle yet significant: Biodiversity of hawkmoth-assemblages (Lepidoptera: Sphingidae) in South-east-Asia. *Biodiversity and Conservation* 15: 465–486.

Bellard, C., C. Leclerc, B. Leroy, M. Bakkenes, S. Veloz, W. Thuiller, and F. Courchamp. 2014. Vulnerability of biodiversity hotspots to global change. *Global Ecology and Biogeography* 23: 1376–1386.

Birdlife International. 2011. *Distribution maps of Birds of the World*. Cambridge: Birdlife International.

Bruno Manser Fonds. 2014. Bruno Manser Fonds—The Sarawak Geoportal.

Bruno Manser Fund. 2012. Sold down the river. How Sarawak Dam Plans compromise the 385 Future of Malaysia's Indigenous Peoples. Technical report.

Ceballos, G., and P.R. Ehrlich. 2002. Mammal population losses and the extinction crisis. *Science* 296: 904–907.

Condit, R., P.S. Ashton, P. Baker, S. Bunyavejchewin, S. Gunatilleke, N. Gunatilleke, S.P. Hubbell, R.B. Foster, et al. 2000. Spatial patterns in the distribution of tropical tree species. *Science* 288: 1414–1418.

de Bruyn, M., B. Stelbrink, R.J. Morley, R. Hall, G.R. Carvalho, C.H. Cannon, G. van den Bergh, E. Meijaard, et al. 2014. Borneo and Indochina are major evolutionary hotspots for Southeast Asian biodiversity. *Systematic Biology* 63: 879–901.

Dengler, J. 2009. Which function describes the species–area relationship best? A review and empirical evaluation. *Journal of Biogeography* 36: 728–744.

Dial, R.J., M.D.F. Ellwood, E.C. Turner, and W.A. Foster. 2006. Arthropod abundance, canopy structure, and microclimate in a Bornean lowland tropical rain forest. *Biotropica* 38: 643–652.

Drakare, S., J.J. Lennon, and H. Hillebrand. 2006. The imprint of the geographical, evolutionary and ecological context on species-area relationships. *Ecology Letters* 9: 215–227.

Ehrlich, P.R., and G.C. Daily. 1993. Population extinction and saving biodiversity. *Ambio* 22: 64–68.

Finer, M., C.N. Jenkins, S.L. Pimm, B. Keane, and C. Ross. 2008. Oil and gas projects in the Western Amazon: Threats to wilderness, biodiversity, and indigenous peoples. *PLoS ONE* 3: e2932.

Forister, M.L., V. Novotny, A.K. Panorska, L. Baje, Y. Basset, P.T. Butterill, L. Cizek, P.D. Coley, et al. 2014. The global distribution of diet breadth in insect herbivores. *Proceedings of the National Academy of Sciences of the United States of America* 112: 442–447.

Gaston, K.J., T.M. Blackburn, and K. Klein Goldewijk. 2003. Habitat conversion and global avian biodiversity loss. *Proceedings of the Royal Society B* 270: 1293–1300.

Gaveau, D.L.A., S. Sloan, E. Molidena, H. Yaen, D. Sheil, N.K. Abram, M. Ancrenaz, R. Nasi, et al. 2014. Four decades of forest persistence, clearance and logging on Borneo. *PLoS ONE* 9: e101654.

Goh, E. 2007. *Developing the Mekong: Regionalism and Regional Security in China-Southeast Asian relations*. London: The International Institute for Strategic Studies.

Harte, J. 2011. *Maximum entropy and ecology: A theory of abundance, distribution, and energetics*. Oxford: Oxford University Press.

Harte, J., and A.P. Kinzig. 1997. On the implications of species–area relationships for endemism, spatial rurnover, and food web patterns. *Oikos* 80: 417–427.

Harte, J., and J. Kitzes. 2015. Inferring regional-scale species diversity from small-plot censuses. *PLoS ONE* 10: e0117527.

Harte, J., T. Zillio, E. Conlisk, and A. Smith. 2008. Maximum entropy and the state-variable approach to macroecology. *Ecology* 89: 2700–2711.

Harte, J., A.B. Smith, and D. Storch. 2009. Biodiversity scales from plots to biomes with a universal species–area curve. *Ecology Letters* 12: 789–797.

He, F., and S.P. Hubbell. 2011. Species–area relationships always overestimate extinction rates from habitat loss. *Nature* 473: 368–371.

Hughes, J.B., G.C. Daily, and P.R. Ehrlich. 1997. Population diversity: Its extent and extinction. *Science* 278: 689–692.

IEA. 2013. *Southeast Asia Energy Outlook*. Paris: International Energy Agency.

IUCN. 2011. The IUCN Red List of Threatened Species. Version 2011.2.

Johnson, J.A. 2012. Assessing the Impact of Climate Change in Borneo. Technical report, World Wildlife Fund, Washington, D.C.

Jones, K.E., J. Bielby, M. Cardillo, S.A. Fritz, J. O'Dell, C.D.L. Orme, K. Safi, W. Sechrest, et al. 2009. PanTHERIA: A species-level database of life history, ecology, and geography of extant and recently extinct mammals. *Ecology* 90: 2648.

Keong, C.Y. 2005. Energy demand, economic growth, and energy efficiency—The Bakun dam-induced sustainable energy policy revisited. *Energy Policy* 33: 679–689.

Kinzig, A.P., and J. Harte. 2000. Implications of endemics–area relationships for estimates of species extinctions. *Ecology* 81: 3305–3311.

Kitching, R.L., D. Li, and N.E. Stork. 2001. Assessing biodiversity 'sampling packages': How similar are arthropod assemblages in different tropical rainforests ? *Biodiversity and Conservation* 10: 793–813.

Kitzes, J. A. 2012. Quantitative ecology and the conservation of biodiversity: Species richness, abundance, and extinction in human-altered landscapes. Doctoral dissertation, University of California, Berkeley.

Kitzes, J., and J. Harte. 2014. Beyond the species–area relationship: Improving macroecological extinction estimates. *Methods in Ecology and Evolution* 5: 1–8.

Koh, L.P., and J. Ghazoul. 2010. A matrix-calibrated species–area model for predicting biodiversity losses due to land-use change. *Conservation Biology* 24: 994–1001.

Koh, L.P., T.M. Lee, N.S. Sodhi, and J. Ghazoul. 2010. An overhaul of the species–area approach for predicting biodiversity loss: Incorporating matrix and edge effects. *Journal of Applied Ecology* 47: 1063–1070.

Koh, L. P., C. J. Kettle, D. Sheil, T. M. Lee, X. Giam, L. Gibson, and G. R. Clements. 2013. Biodiversity state and trends in southeast Asia. In *Encyclopedia of biodiversity*, ed. S.A. Levin, vol. 1, 509–527. Amsterdam: Elsevier.

Lee, T., T. Jalong, and W. Meng-Chuo. 2014. *No consent to proceed: Indigenous Peoples' Rights Violations at the Proposed Baram Dam in Sarawak*. Sarawak: Save Sarawak Rivers Network (SAVE Rivers).

Losos, E., and E.G. Leigh, Jr., eds. 2004. *Tropical forest diversity and dynamism: Findings from a large-scale plot network*. Chicago, IL: University of Chicago Press.

May, R.M., J.H. Lawton, and N.E. Stork. 1995. Assessing extinction rates. In *Extinction rates*, ed. J.H. Lawton, and R.M. May, chap. 1, 1–24. Oxford: Oxford University Press.

McGlinn, D.J., X. Xiao, and E.P. White. 2013. An empirical evaluation of four variants of a universal species–area relationship. *PeerJ* 1: e212.

Millennium Ecosystem Assessment. 2005. *Ecosystems and human well-being: Synthesis*. Washington, D.C.: Island Press.

Myers, N., R.A. Mittermeier, C.G. Mittermeier, G.A. da Fonseca, and J. Kent. 2000. Biodiversity hotspots for conservation priorities. *Nature* 403: 853–858.

Ney-Nifle, M., and M. Mangel. 2000. Habitat loss and changes in the species–area relationship. *Conservation Biology* 14: 893–898.

OECD. 2013. *Economic Outlook for Southeast Asia, China and India 2014: Beyond the Middle Income Trap*. Paris: OECD Publishing.

Rosenzweig, M.L. 1995. *Species diversity in space and time*. Cambridge: Cambridge University Press.

Sarkar, S., R.L. Pressey, D.P. Faith, C.R. Margules, T. Fuller, D.M. Stoms, A. Moffett, K.A. Wilson, et al. 2006. Biodiversity conservation planning tools: Present status and challenges for the future. *Annual Review of Environment and Resources* 31: 123–159.

Sodhi, N.S., L.P. Koh, R. Clements, T.C. Wanger, J.K. Hill, K.C. Hamer, Y. Clough, T. Tscharntke, et al. 2010. Conserving Southeast Asian forest biodiversity in human-modified landscapes. *Biological Conservation* 143: 2375–2384.

Sovacool, B.K., and L. Bulan. 2011. Behind an ambitious megaproject in Asia: The history and implications of the Bakun hydroelectric dam in Borneo. *Energy Policy* 39: 4842–4859.

Sovacool, B.K., and L. Bulan. 2012a. Energy security and hydropower development in Malaysia: The drivers and challenges facing the Sarawak Corridor of Renewable Energy (SCORE). *Renewable Energy* 40: 113–129.

Sovacool, B.K., and L.C. Bulan. 2012b. They 'll be dammed: the sustainability implications of the Sarawak Corridor of Renewable Energy (SCORE) in Malaysia. *Sustainability Science* 8: 121–133.

Stork, N. 2015. The composition of the arthropod fauna of Bornean lowland rain forest trees. *Journal of Tropical Ecology* 7: 161–180.

Struebig, M.J., A. Wilting, D.L. Gaveau, E. Meijaard, R.J. Smith, M. Fischer, K. Metcalfe, and S. Kramer-Schadt. 2015. Targeted conservation to safeguard a biodiversity hotspot from climate and land-cover change. *Current Biology* 25: 372–378.

Thomas, C.D., A. Cameron, R.E. Green, M. Bakkenes, L.J. Beaumont, Y.C. Collingham, B.F.N. Erasmus, M.F. De Siqueira, et al. 2004. Extinction risk from climate change. *Nature* 427: 145–148.

Whitmore, T. and I. Tantra. 1987. The flora of Indonesia: Draft checklist for Borneo. Technical report, Forest Research and Development Centre, Bogor, Indonesia.

Wilber, M.Q., J. Kitzes, and J. Harte. 2015. Scale collapse and the emergence of the power law species-area relationship. *Global Ecology and Biogeography* (Advance Online Publication).

AUTHOR BIOGRAPHIES

Justin Kitzes (✉) is a postdoctoral scholar in the Energy and Resources Group and a data science fellow at the Berkeley Institute for Data Science, both at the University of California, Berkeley. He is a theoretical and applied ecologist who works to develop general

quantitative approaches to predict the effects of global change on biodiversity.
Address: Energy and Resources Group, University of California, Berkeley, 310 Barrows Hall, Berkeley, CA 94720-3050, USA.
e-mail: jkitzes@berkeley.edu

Rebekah Shirley is currently a Ph.D. student with the Energy and Resources Group at the University of California, Berkeley, where she also obtained a M.Sc. Energy Resources and a M.Sc. Civil Engineering. She focuses on power systems analysis, and her research involves building energy management and decision-support tools for developing countries, particularly Small Island Developing States. Rebekah is a University of California Chancellor's Fellow.
Address: Energy and Resources Group, University of California, Berkeley, 310 Barrows Hall, Berkeley, CA 94720-3050, USA.
e-mail: rebekah.shirley@berkeley.edu