



Conservation biogeography of the US–Mexico border: a transcontinental risk assessment of barriers to animal dispersal

Jesse R. Lasky^{1*}, Walter Jetz^{2,3} and Timothy H. Keitt¹

¹Section of Integrative Biology, University of Texas at Austin, 1 University Station C0900, Austin, TX 78712-0253, ²Ecology and Evolutionary Biology Department, Yale University, 165 Prospect Street, New Haven, CT 06520, ³Division of Biological Sciences, University of California, San Diego, 9500 Gilman Drive, MC 0116, La Jolla, CA 92093-0116, USA

ABSTRACT

Aim Humans have dramatically transformed landscapes along the US–Mexico border. We aim to assess the risk of barriers that may significantly impede animal migrations within this ecologically sensitive region.

Location United States and Mexico.

Methods We examined the intersection of current and possible future barriers along the border with the geographic ranges of 313 amphibian, reptile and non-volant mammal species. We considered the areas of intensive human land use and ~ 600 km of pedestrian fence as current barriers along the border. We evaluated the impacts of two scenarios of dispersal barriers – continuation of existing and construction of new barriers – and identified species vulnerable to global and local extinction.

Results Among the species most at risk from current barriers are four species listed as threatened globally or by both nations, 23 species for which the larger of their two national subranges is < 10⁵ km² and 29 species whose ranges cross the border only marginally. Three border regions, California, Madrean archipelago and Gulf coast, emerge as being of particular concern. These regions are characterized by high overall species richness and high richness of species at risk from existing barriers and from construction of potential new barriers.

Main conclusions New barriers along the border would increase the number of species at risk, especially in the three identified regions, which should be prioritized for mitigation of the impacts of current barriers. The species we identified as being potentially at risk merit further study to determine impacts of border dispersal barriers.

Keywords

Border fence, endemic species, northern Mexico, range margins, southwestern US, species range maps, threatened species, transboundary conservation.

*Correspondence: Jesse R. Lasky, Section of Integrative Biology, University of Texas at Austin, 1 University Station C0900, Austin, TX 78712-0253, USA.
E-mail: jesserlasky@mail.utexas.edu

INTRODUCTION

The US–Mexico border bisects North America and is marked by intensive human land use and ~ 1200 km of recently constructed barriers to human migration. These modifications may severely threaten the diverse wildlife of the region (Cohn, 2007; de la Parra & Córdova, 2007; Sayre & Knight, 2010). Anthropogenic impacts are expected to increase with future land use change and further expand fences and walls along the border (Fleisch *et al.*, 2010). The problem of anti-immigration

barriers is particularly severe as US law exempts their construction from adherence to all environmental regulatory and review requirements (US Library of Congress (USLOC), 2005b). Under the REAL ID Act of 2005, the Secretary of the Department of Homeland Security (DHS) has authority to construct barriers across the entire border at any time without oversight of environmental regulatory law. To date, a binational, transcontinental analysis of the potential threats facing the border fauna, including those posed by dispersal barriers, is lacking.

The US–Mexico border lies roughly east–west across North America, while the mountain ranges of the border region (Sierra Madre Occidental, Sierra Madre Oriental, California Coastal) run roughly north–south, so that the border crosses the mountain ranges at approximately a 70° angle. These mountain chains exhibit high spatial heterogeneity in precipitation (National Atlas, 2008) and bound major ecosystems, some of which occur in narrow bands [Commission for Environmental Cooperation (CEC), 1997]. As a result, even short anthropogenic barriers along the border could bisect ecosystems and species ranges.

Barriers across large portions of species' ranges may negatively impact populations. Theoretical (e.g. Levins, 1970) and empirical (e.g. Epps *et al.*, 2005) research demonstrates that dispersal barriers need not be entirely impermeable to have strong effects on populations. Species with poor dispersal across the border might have reduced gene flow between populations (Keller & Largiader, 2003), which can lead to drift-caused genetic divergence between populations (Mills & Allendorf, 1996) and rapid loss of genetic diversity in small isolated populations (Epps *et al.*, 2005; Jacquemyn *et al.*, 2009). Smaller isolated populations may also be subject to an increased risk of extinction (Shaffer, 1981; Pimm, 1991; Purvis *et al.*, 2000). Populations near species' range margins are often of low density (Brown, 1984) and might be similarly vulnerable if isolated by dispersal barriers. Even slight decreases in dispersal may have large consequences for species' populations such as extinction of a low-density metapopulation (Levins, 1970).

There are at least three major types of anthropogenic barriers to cross-border animal dispersal: human-altered landscapes, fences and walls, and areas of high human activity (Cohn, 2007; Spangle, 2007). Rapid construction of fences began after US President George W. Bush signed legislation mandating ~ 1200 km of fencing along the US–Mexico border (Fletcher & Weisman, 2006; USLOC, 2006). These barriers, owing to their linear nature, have a great potential per unit length to bisect populations. Of the two border fence types (vehicle and pedestrian), we focus on potential impacts of pedestrian fences, which currently extend ~ 600 km and are intended to be impermeable to humans [US Government Accountability Office (GAO), 2009]. These fences and walls are typically at least 4.5 m tall, sunk 1 m into the ground and have either no openings or openings of 1–10 cm (US DHS, 2008a). Human disturbance, vegetation removal and additional barriers, roads and lighting that accompany fences (Spangle, 2007; US Government Printing Office, 2008) likely further reduce border permeability where fences are installed (Trombulak & Frissell, 2000; Cohn, 2007; Flesch *et al.*, 2010; Sayre & Knight, 2010). Co-occurring in the region are extensive anthropogenic landscapes that are home to a rapidly growing population of ~ 12 million people (Stoleson *et al.*, 2005; US–Mexico Border Health Commission, 2009). Such highly urbanized landscapes likely have low suitability and permeability for native species (Harrison, 1997; Trombulak & Frissell, 2000; McKinney, 2002; Epps *et al.*, 2005).

Researchers have designated the most important areas in the Mexican border region for the conservation of species threatened in Mexico (Koleff *et al.*, 2007). However, a comprehensive binational analysis of species-level risk from barriers in the region is lacking. This study is the first large-scale evaluation of the threats posed by border dispersal barriers to non-volant terrestrial vertebrates. Ideally, evaluations of the risk of barriers would incorporate detailed data on species' movements, as was carried out for jaguar (*Panthera onca*; McCain & Childs, 2008) and desert bighorn sheep (*Ovis canadensis mexicana*; Flesch *et al.*, 2010). Few data exist, however, for the great majority of the ~ 300 species of amphibians, reptiles, and non-volant mammals found at the border. In the absence of such data, we estimated risk by examining species range maps and resulting biogeographic patterns.

Dispersal barriers can have impacts at multiple levels of ecological organization. Our approach proceeds in a top-down fashion from ecoregions, which represent relatively self-contained biogeographical units, to assemblages of varying richness and composition along the border, to individual species at the most basic unit. In each case, we characterize the extent to which barriers intersect these units. The conservation objectives of these analyses were to (1) prioritize regions for the conservation of transborder connectivity and (2) identify species at risk meriting further study.

Our species-level analysis centred around two related aspects of risk: (1) loss of population interconnectivity owing to a reduction in dispersal across the border and (2) reduction in effective population sizes subsequent to loss of connectivity. It is important to recognize that these components of risk can operate both locally and range-wide depending on the size of a species range and its location relative to barriers. Relevant scenarios are summarized in Fig. 1. At the global scale, we deem two groups of species as most at risk. First, species already listed as threatened by the International Union for the Conservation of Nature (IUCN) or by both the US and Mexican governments are at risk from a loss of connectivity (risk G1, Fig. 1). Second, species with small geographic ranges that are bisected into evenly sized populations are at high risk because this scenario produces the smallest remnant

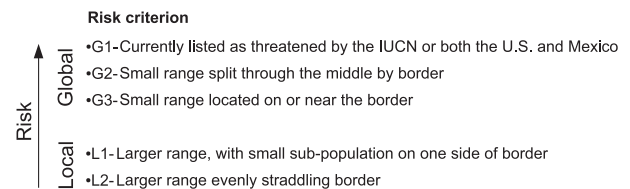


Figure 1 Criteria of species range size and location used to estimate relative risk to species' global and local populations from barriers along the border. G1, G2 and L1 are species considered at risk to hypothetical extensive barriers. G3 species are at risk globally from general disturbances. L2 species are considered least at risk from range bisection. Note that categories are not mutually exclusive.

populations and ranges (risk G2). Species with small ranges are typically at greater risk of extinction than large-ranged species (Purvis *et al.*, 2000). At a local scale, we associate risk with remnant populations that are separated from the rest of the species range by barriers along the border (risk L1). Such geographically marginal populations are often of low density (Brown, 1984) and vulnerable to anthropogenic change. These marginal populations, while not necessarily of global conservation concern when the overall range is large, are important in the context of local ecosystems. Within this framework, we evaluate risk stemming from range bisection under two scenarios: (1) risk posed by bisecting a species range, a hypothetical scenario that may result from extensive barriers in the future and (2) risk from current conditions of land use and implementation of barriers that threaten to bisect ranges.

METHODS

Data sources

Digital range maps of ecoregions (CEC, 1997) and amphibian (IUCN, 2008), reptile (Conant & Collins, 1998; Stebbins, 2003; IUCN, NatureServe, and Conservation International, 2007) and non-volant mammal species (Patterson *et al.*, 2007) were used in all analyses, which were computed in ARC GIS 9.2 (ESRI). We digitized the locations of pedestrian border fences already constructed or planned by US Customs and Border Protection (CBP) as of 1 January 2011 (data primarily from governmental sources, see Appendix S1 in Supporting Information). We included fences with either no openings or openings 1–10 cm and that are ~ 4.5 m tall and sunk 1 m into the ground, although precise specifications are often not available for individual sections of fence (US DHS, 2008a; see Appendices S1 and S2). We did not include the older three-strand barbed wire fences that are installed along much of the border because information on their locations is scarce. Nearly all of the fence sections included in analyses have already been constructed as of 1 January 2011, save some segments totalling < 20 km in the lower Rio Grande Valley (US CBP, 2009). Pedestrian fencing extends over 21% of the total length of the border and is most prevalent near the coasts.

Areas of intensive human land use are found scattered across the border, such as the San Diego/Tijuana, Nogales and El Paso/Juarez urban areas and the urban/agricultural Rio Grande Valley. Dispersal-limiting anthropogenic landscapes along the border were identified using the Human Footprint Index (HFI), a metric of human impact on ecosystems (Sanderson *et al.*, 2003). Impacts were estimated using data on human population density, access (via roads, railroads, and navigable bodies of water), night-time lights, urbanization and agriculture (Sanderson *et al.*, 2003). Relative human impacts were calculated for each 30 arc-second cell and then normalized to a scale of 0–100 for each biome (Sanderson *et al.*, 2003). We then averaged HFI values across a 20-km-wide strip about the border for 1-km segments of the border. The width of the 20-km strip was chosen to encompass the range of variation in the

size of border urban areas. The choice of the top quartile was arbitrary, but thresholds between the 65th and 95th percentiles identify the same urban centres as barriers. Varying this threshold has little effect because of the large difference in human impact between urbanized vs. non-urbanized areas along the border.

We evaluated species risk from two scenarios of border barriers. The first scenario is the current situation at the border, defined by the existing (or imminent) barriers. ‘Current barriers’ were defined as locations having pedestrian fence or top quartile HFI. We included existing pedestrian fences, in addition to some short pedestrian fence segments (totalling < 20 km) currently under construction or having specific construction plans (US CBP, 2009). We used this scenario to identify species most at risk because of range bisection by current barriers; hereafter, we refer to this scenario as one of ‘current barriers.’ The second scenario, which is hypothetical, is defined by barriers extensive enough to effectively bisect a species range. We used this scenario to identify species most at risk from range bisection by any extensive border barriers; hereafter, we refer to this scenario as one of ‘extensive barriers.’ The second scenario may be currently faced by species with extensive barriers across their range, or it may be a potential future scenario for any species.

Quantifying regional biogeographic patterns

It is instructive to examine the intersection of ecoregions (Level III, CEC, 1997), whose boundaries are roughly coincident with many species’ range edges, and the border. Ecoregional patterns can be representative of biogeographic patterns across many species, including those for which data are lacking (Feeley & Silman, 2009). We measured the width of ecoregions along the border and the length of current barriers contained within them.

Using range maps, we tallied the regional richness of all amphibian, reptile and non-volant mammal species, limited to species found within 50 km of the border. Comparisons between local survey data and range maps suggest that expert opinion range maps drawn at continental scales (i.e. our data sets) have rapidly decreasing accuracy at grain sizes below 100 km (Hurlbert & Jetz, 2007). We therefore aggregated species richness within moving, 50-km-radius circular windows. The 50-km radius is a reasonable trade-off between resolving variation in diversity and the small-scale error common in range maps. We measured richness of all species found within 50 km of the border, rather than merely of species having range maps intersecting the border, because of the previously mentioned error in range maps. Our use of overlapping circles diminishes an artefact (aliasing) that may arise when sampling a continuous signal in discrete intervals. Depending on where a grid is anchored, non-overlapping grid cells may show signal variation that is an artefact of variation at much smaller scales than grid cells.

We examined how the richness of border assemblages was related to the occurrence of current barriers. We compared the

observed relationship between richness and the location of current barriers to a null expectation where the occurrence of barriers and richness are independent. We calculated the richness of all border species within 50-km windows centred at 1-km intervals on the border. We calculated the cumulative sum of barrier lengths coinciding with all assemblages with richness less than or equal to a given value. We then generated a null expectation of the accumulation of barriers based on the assumption that barriers were evenly distributed across the border irrespective of richness. Finally, we visually compared the observed cumulative distribution to the null to assess whether richness and barriers were independent.

Complementarity, or uniqueness, of local species assemblages is useful to identify locations that contribute most to preserving total species richness across many locations (Williams *et al.*, 1996). As a measure of complementarity, we identified which local assemblages most differed from the average border assemblage. Local assemblages with the greatest difference from the border-wide average (and thus the highest complementarity) may be prioritized for conservation. Negative impacts of border barriers on relatively unique assemblages would be difficult to offset by conservation at other locations with more typical assemblages. We first identified the composition of local assemblages within 50-km windows centred at 1-km intervals on the border. We then created an average border-wide assemblage based on species relative frequencies of occurrence. For the average border-wide assemblage, each species received a value equal to the frequency of its occurrence in local border assemblages divided by the total number of local assemblages. We then computed the Hellinger distance between all local assemblages and the border-wide average assemblage to estimate the complementarity of each local assemblage.

Assessing species-level risk

We used species range maps and their relation to the border to determine which species are most at risk at global and local levels. Species were further classified according to the scenario in which they were at risk. The species at risk from general extensive barriers across their range are referred to below as 'at risk in a scenario of extensive barriers,' while those at risk from current border impermeability are referred to as 'at risk from current barriers.' Current border permeability for a given species was estimated as the proportion of border in a species range occupied by current barriers (length of border occupied by barriers in range divided by total border length in its range).

Assessment of global risk

We assessed threats because of range bisection by barriers to species already considered vulnerable by conservation agencies. The statuses of species were taken from the Secretaría del Medio Ambiente y Recursos Naturales of Mexico (SEMARNAT, 2002), the US Fish and Wildlife Service (USFWS) (2009), and the IUCN (2008).

We also developed two proxies for relative global risk. First, we used global range area as an indicator of endemics at risk from general disturbances. Second, for species with their range bisected at the border, persistence may depend on the larger of the two remnant subranges. Thus the relative risk posed by range bisection was estimated using the size of a species' largest subrange north or south of the border. This metric may also be interpreted as indicating risk from failure of management in one nation. If management failure results in extinction in the smaller subrange, then the size of the larger remaining subrange indicates the subsequent global risk.

We considered two groups of species globally at the greatest risk in the extensive barriers scenario: (1) species considered vulnerable by the IUCN or both federal conservation agencies (risk G1, Fig. 1) and (2) species with their largest subrange on either side of border $< 10^5$ km² (risk G2, Fig. 1). We identified the subset of species at risk from extensive barriers that are threatened by current barriers. If barriers occupied over 50% of a G1 or G2 species' border range, they were considered at risk from current barriers. We used these arbitrary thresholds to identify the species most at risk.

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Assessment of local risk on one side of the border

We assessed risk to subpopulations at their species range margin near the border. We determined range margin status by calculating the greatest distance between the border and the species range edge north and south of the border. The lesser of these two distances was then divided by the greater, giving a ratio that approaches 0 for species for which the border passes through their range margin to unity for species for which the border passes through the centre of their range. Species were considered as locally at risk in the scenario of extensive barriers if this ratio was < 0.15 (risk L1, Fig. 1). A subset of at risk L1 range margin species was considered at risk from current barriers if barriers occupied over 50% of their border range. Again, thresholds were arbitrary, used to identify the species at the greatest relative risk.

Richness of species at risk

Having identified species most at risk globally and locally because of general extensive and current barriers, we prioritized regions for the preservation of transborder connectivity by measuring their richness. The richness of species at risk in a scenario of future extensive barriers (risks G1, G2 and L1) and of the subset of G1, G2 and L1 species at risk from current barriers was calculated. Richness of species at risk was measured in a circle of radius 50 km sliding along the border. We identified ecoregions rich in species at risk by intersecting ecoregion and species range maps. Although we used arbitrary thresholds of risk, more stringent thresholds yielded consistent geographic patterns of species risk. We also measured richness

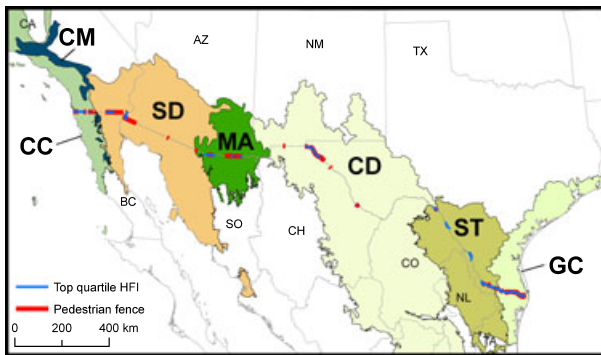


Figure 2 Ecoregions found in both the US and Mexico (CEC, 1997), with pedestrian fences (red) and areas of high Human Footprint Index (blue). Ecoregions are: CC, California coastal; CM, California/Baja California Mountains; SD, Sonoran Desert; MA, Madrean Archipelago; CD, Chihuahuan Desert; ST, South Texas/Interior Plains and GC-Western Gulf Coastal Plain. States (grey lines) are as follows: CA, California; AZ, Arizona; NM, New Mexico; TX, Texas; BC, Baja California; SO, Sonora; CH, Chihuahua; CO, Coahuila; NL, Nuevo Leon; TA, Tamaulipas.

of species in different overall range size categories to indicate regions harbouring the most endemic species with small overall ranges and that are sensitive to disturbance in general (risk G3).

RESULTS

Regional biogeography and barriers

Seven ecoregions are found on both sides of the border (Fig. 2, CEC, 1997). Pedestrian fencing is most common in the California and Gulf coastal ecoregions, where 62% and 48% of the border is occupied by pedestrian fences, respectively. These were also the two narrowest ecoregions as measured along the border. Areas of high human impact were present in every ecoregion. Border areas in the top quartile of HFI occupy 25% of the border length. Sections with pedestrian fencing often co-occur, but also considerably extend, the barriers represented by high HFI. Combined, these barriers span 975 km or 34% of the border.

Vertebrate groups attained high regional richness in different locations along the border (Table 1). Mammals and reptiles were most species-rich in the Madrean archipelago/Chihuahuan desert, while amphibians were most species-rich in the Rio Grande Valley/central Texas (Fig. 3). Range maps showed that 57 amphibian, 178 reptilian, and 134 mammalian species occur within 50 km of the border, with border fence intersecting the ranges of 38, 152 and 113 species, respectively (see Appendix S3). Amphibian species occurring at the border comprise 17% of amphibian species within the entire US and 16% of amphibian species within all of Mexico, border reptiles comprise 49% of the US reptilian fauna (NatureServe 2011) and 18% of the Mexican reptilian fauna (CONABIO 2011), and border mammals comprise 39% of the US mammalian

fauna and 40% of the Mexican mammalian fauna. Barriers were more likely to occur among assemblages of moderate species richness, relative to the null expectation based on random placement of barriers (Fig. 4). The extreme lowest and highest diversity assemblages co-occurred with barriers at a rate similar to the null expectation. Among species, an average of 28% (SD = 18) of the border length dissecting species' ranges was occupied by pedestrian fence and 41% (SD = 24) by pedestrian fence or areas of high HFI. Thus, pedestrian fences and combined pedestrian fences and areas of high HFI occupy lower percentages of the border as a whole (21% and 34%, respectively) than the average length they occupy within species ranges (28% and 41%, respectively). This difference indicates that barriers are not located at random relative to species ranges and that barriers are more common in areas rich in species with small ranges (Fig. 5).

Complementarity of local assemblages was greatest in the Gulf Coastal Plain, signifying that these assemblages were most different from the border-wide average than any other assemblages (Fig. S1). Complementarity also peaked at the California coastal ecoregion, while the middle portion of the continent had the lowest complementarity.

Global risk

Fifty species and three subspecies that are globally threatened (IUCN, 2008) or federally threatened in Mexico or the US (SEMARNAT, 2002; USFWS, 2009) occur within 50 km of the border. The scenario of hypothetical extensive barriers increases risk for the 14 IUCN or binationally threatened species that are found at the border (risk G1). These species, at risk from extensive barriers, peak in richness along the Arizona border, near the boundary between the Sonoran Desert and Madrean Archipelago (Fig. 5). Of the IUCN or binationally threatened species, we consider five coastal species to be most at risk from current barriers (i.e. barriers occupy over 50% of the border length in range; Table 2, Fig. 5).

Endemic species with small geographic range size are particularly at risk from both natural and anthropogenic disturbances. Richness of this group was greatest near the coasts and in the Madrean archipelago region (risk G3, Fig. 5). We considered species globally at risk from extensive barriers if, when their range was bisected at the border, the larger remaining subrange north or south of the border was $< 10^5 \text{ km}^2$ (risk G2). We identified 45 such small subrange species (Fig. 6). Nearly all IUCN threatened species had relatively small remaining subranges. The Sonoran Desert and California coastal ecoregions contained the greatest richness of species with small remaining subranges (Table 1), consistent with variation in species total range size (Fig. 5). Twenty-three of the 45 small subrange species were considered most at risk because of current barriers (i.e. over 50% of the border within their range occupied by barriers; Table 2, Fig. 6). These species were found mainly in the California Coastal and Sonoran Desert ecoregions, which have extensive dispersal barriers (Table 1, Fig. 5). Species with large

Table 1 The richness of all non-volant species and of species potentially at risk, identified by analyses of range maps, in the six border ecoregions.

	Ecoregion	CC	SD	MA	CD	ST	GC
All species	Amphibian	12	26	18	24	24	21
	Reptile	60	102	82	104	81	54
	Mammal	55	94	78	90	67	49
	Total	127	222	178	218	172	124
<i>Vulnerability criterion</i>							
IUCN threatened or threatened in both nations	Amphibian	2	3	1	1	1	1
	Reptile	1	3	2	2	1	1
	Mammal	0	3	4	3	3	2
	Total	3	9	7	6	5	4
IUCN threatened or threatened in both nations and > 50% border range with barriers	Amphibian	2	2	0	0	1	1
	Reptile	1	1	0	0	0	0
	Mammal	0	1	1	0	1	1
	Total	3	4	1	0	2	2
Larger subrange < 10 ⁵ km ²	Amphibian	2	3	1	1	2	2
	Reptile	13	18	4	10	6	4
	Mammal	6	9	2	3	0	0
	Total	21	30	7	14	8	6
Larger subrange < 10 ⁵ km ² and > 50% border range with barriers	Amphibian	2	2	0	1	2	2
	Reptile	9	10	0	1	2	2
	Mammal	6	7	1	0	0	0
	Total	17	19	1	2	4	4
Near range margin	Amphibian	2	2	0	4	8	8
	Reptile	11	14	10	18	14	13
	Mammal	10	19	16	19	13	13
	Total	23	35	26	41	35	34
Near range margin and > 50% border with barriers	Amphibian	2	2	0	3	7	7
	Reptile	7	7	2	4	6	6
	Mammal	4	6	2	3	3	3
	Total	13	15	4	10	16	16

Note that ecoregions vary widely in extent, and thus richness in regions of equal area showed different geographical patterns (Figs 3 & 4). Species considered at risk from future extensive barriers are as follows: (1) those already considered vulnerable by the IUCN or both the US and Mexico (risk G1), (2) those with small remaining subranges (risk G2, larger subrange < 10⁵ km²) and (3) those near range margins (risk L1, ratio of distances from border to range edges < 0.15). Species from these two groups are considered at risk from current barriers if over 50% of their border range is occupied by current barriers. CC, Coastal California; SD, Sonoran Desert; MA, Madrean Archipelago; CD, Chihuahuan Desert; ST, Southern Texas Plains; GC, Gulf Coastal Plain.

remaining subranges tended to have proportionally less of their range occupied by current dispersal barriers (Fig. 6).

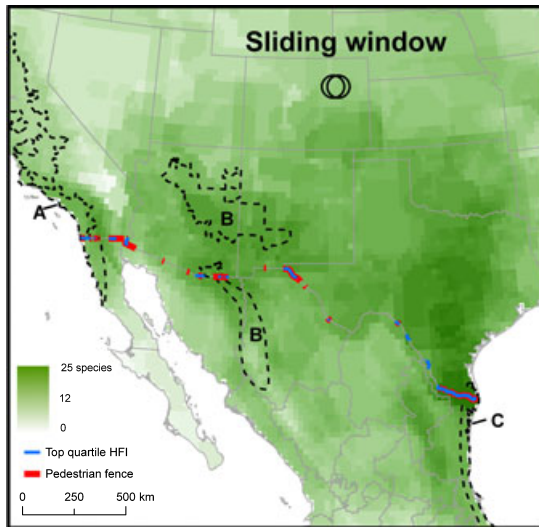
Local risk on either side of border

Dispersal barriers potentially threaten populations near their species range margin at the border with local extinction in one nation. Range margin species were identified by the symmetry of their range about the border, calculating the ratio of maximum distances between the border and two range edges (N and S of the border). Species were considered at their range margins if the lesser of these two distances divided by the greater was < 0.15. In total, there were 65 species at their range margin near the border, species that are locally at risk in a scenario of extensive barriers across their range (risk L1). Such

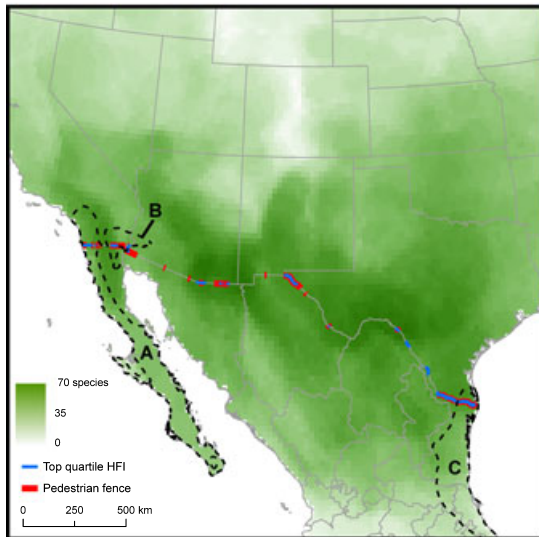
species include 10 nationally threatened species and two globally IUCN threatened species (Fig. 6). Range margin species were more likely to be classified as federally threatened by the US or Mexican governments (17%) than non-range margin species (12%); this difference was nearly statistically significant at $\alpha = 0.05$ ($\chi^2 = 3.367$, $P = 0.067$). The higher level of officially recognized risk for range margin species supports our contention that species near their range margins at the border represent potentially vulnerable subpopulations. Dozens of range margin species were found within each ecoregion, with total range margin species richness peaking in the Gulf Coastal Plain (Fig. 5).

Of the 65 range margin species at the border, 29 species were considered most at risk from current barriers (i.e. over 50% of the border within their range occupied by barriers) and 16 of

(a) Amphibians



(b) Reptiles



(c) Mammals

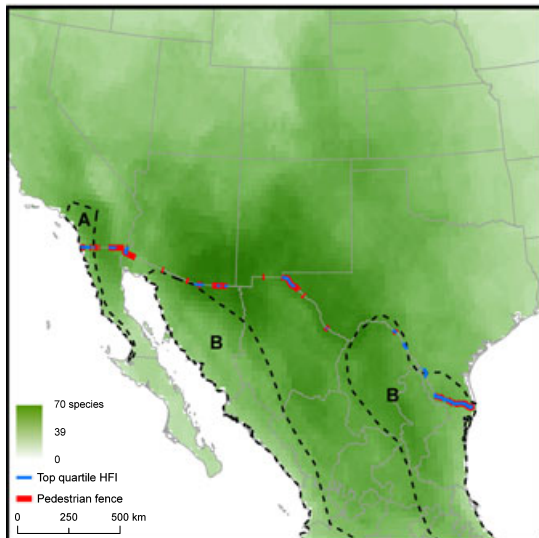


Figure 3 Species richness of (a) amphibians, (b) reptiles and (c) non-volant mammals along the US–Mexico border, with pedestrian fences (red) and areas of high Human Footprint Index (blue). Richness was tallied within sliding, 50-km-radius circles. Species whose closest range margin fell outside a 50-km buffer along the border were excluded. Our analysis likely overestimates local richness because range maps typically do not capture fine-scale patchiness in species occurrence. Dotted lines show species' ranges with large portions intersected by fences (a) A-*Spea hammondi*, B-*Hyla wrightorum* and C-*Rhinophrynus dorsalis*; (b) A-*Aspidosclis hyperythra*, B-*Uma notata* and C-*Coniophanes imperialis*; and (c) A-*Chaetodipus fallax* and B-*Leopardus pardalis*.

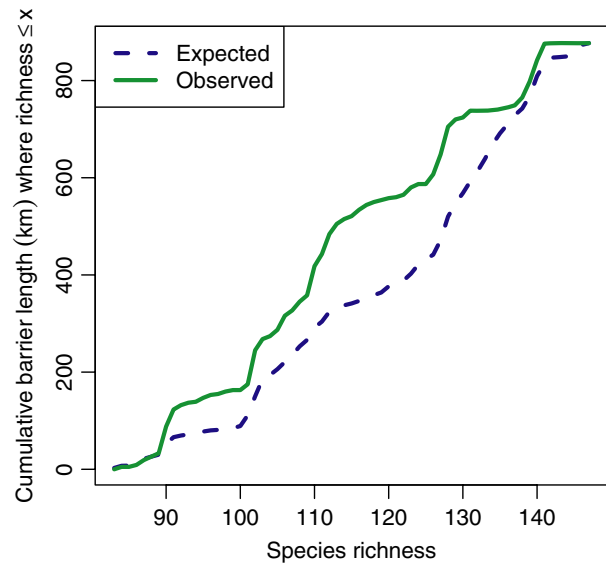


Figure 4 Cumulative barrier length in all assemblages of richness $\leq x$. The expected distribution assumes that barriers occur independently of the species richness of assemblages.

these species had barriers across over 75% of their range (Table 2, Fig. 6). Range margin species with extensive barriers in their range were principally found towards the coasts (Fig. 5). The ranges of both small subrange size species and species near the edge of their range cross the border for relatively short lengths (data not shown), so that a scenario of barriers bisecting their ranges is highly plausible.

DISCUSSION

Biogeography, species at risk and regions of the border

To prioritize regions for coordinated binational conservation and preservation of transborder connectivity, we have identified regions rich in all border species and species most at risk globally and locally. We place the highest priority for mitigation of the impacts of barriers on species identified as at risk under the scenario of current barriers, because these species are confronted with existing barriers. We place the highest priority for the preservation of future transborder

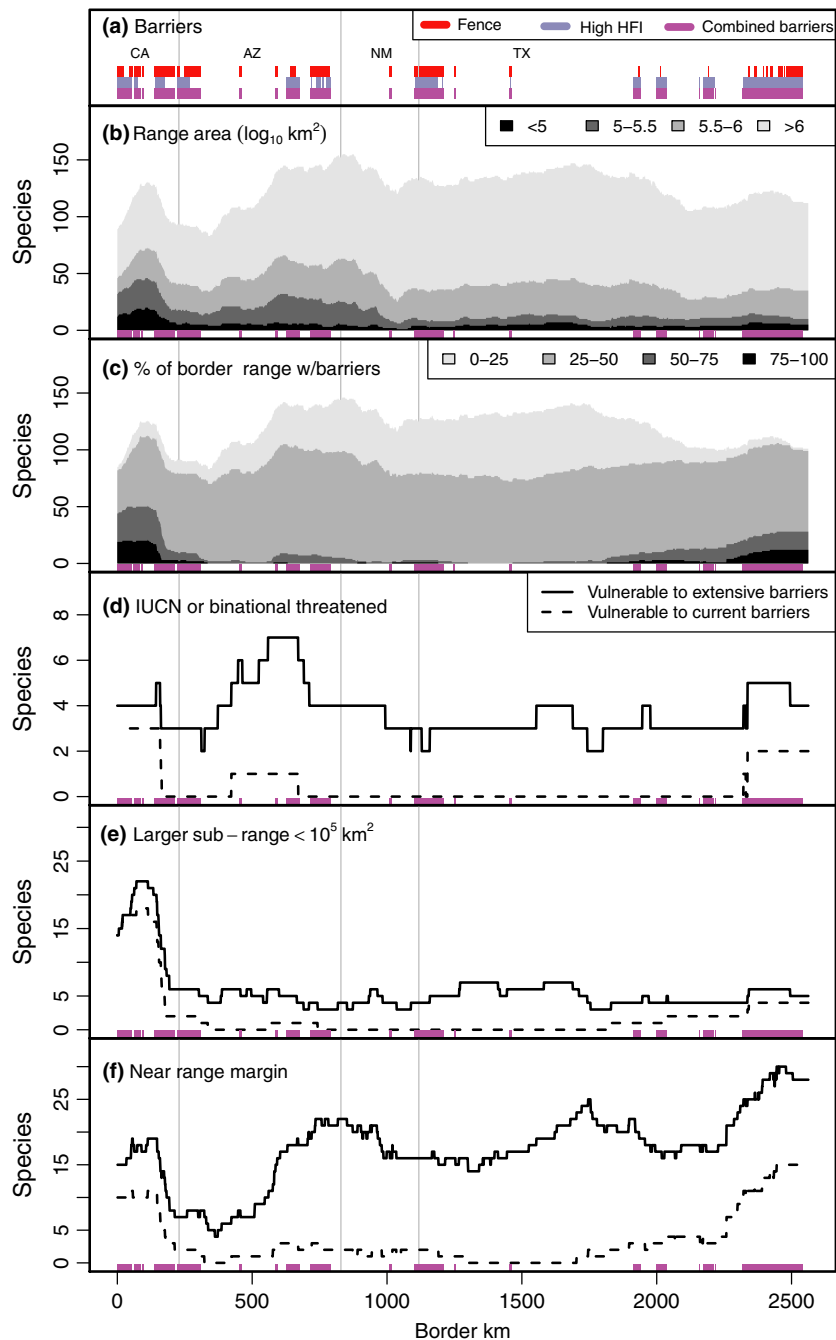


Figure 5 (a) Longitudinal views of potential barriers, (b–c) range characteristics of all species, used to illustrate range characteristics for all border species, and (d–f) richness of species most at risk from barriers along the border. (a) Locations of pedestrian fence (red), areas of top quartile Human Footprint Index (blue) and both current barriers (purple). (b) Stacked area view of the total range area of all species found at the border. (c) Stacked area view of the percent of species’ border range occupied by current barriers (length of barriers in range/length of border in range). (d) Richness of species globally at risk because of classification as threatened by the IUCN or both nations: those at risk from potential extensive future barriers (G1, solid lines) and the subset at risk from current barriers (dashed lines). (e) Richness of species globally at risk because of isolation by barriers into small subranges (G2), risk scenarios shown as in (d). (f) Richness of species at their range margin along the border and locally at risk (L1), risk scenarios shown as in (d). The view is longitudinal from west to east across the border.

connectivity on the species at risk under the hypothetical scenario of extensive barriers that are not at risk from current barriers. The risk to this latter group of species is hypothetical and could emerge if future barriers are constructed within their

ranges. The regions of the greatest richness of species at risk from both scenarios indicate where current or future barriers would have the most dramatic impacts on vertebrate assemblages (Fig. 5). The regions of highest border species richness

Table 2 Species identified as potentially at risk from current border dispersal barriers.

Family	Species	English names	IUCN or binational threatened and border barrier > 50% of range	Larger subrange < 10 ⁵ (km ²) and border barrier > 50% of range	Range margin and border barrier > 50% of range
<i>Amphibians</i>					
Bufonidae	<i>Anaxyrus boreas</i>	Western toad			
Bufonidae	<i>Anaxyrus californicus</i>	Arroyo toad	IUCN-E	X	
Bufonidae	<i>Rhinella marina</i>	Giant marine toad			X
Eleutherodactylidae	<i>Eleutherodactylus cystignathoides</i>	Rio Grande chirping frog		X	
Hylidae	<i>Pseudacris clarkii</i>	Spotted chorus frog			X
Hylidae	<i>Smilisca baudinii</i>	Mexican treefrog			X
Leptodactylidae	<i>Leptodactylus fragilis</i>	American white-lipped frog			X
Microhylidae	<i>Hypopachus variolosus</i>	Sheep frog			X
Plethodontidae	<i>Batrachoseps major</i>	Garden slender salamander		X	
Plethodontidae	<i>Ensatina eschscholtzii</i>	Ensatina			X
Ranidae	<i>Rana draytonii</i>	California red-legged frog	IUCN-V		
Rhinophrynidae	<i>Rhinophrynus dorsalis</i>	Burrowing toad			X
Salamandridae	<i>Notophthalmus meridionalis</i>	Black-spotted newt	IUCN-E	X	
Sirenidae	<i>Siren intermedia</i>	Lesser siren			X
<i>Reptiles</i>					
Colubridae	<i>Coniophanes imperialis</i>	Black-striped snake			X
Colubridae	<i>Gyalopion quadrangulare</i>	Thornscrub hook-nosed snake			X
Colubridae	<i>Ophedrys aestivus</i>	Rough greensnake			X
Colubridae	<i>Tantilla planiceps</i>	Western black-headed snake		X	
Colubridae	<i>Thamnophis hammondi</i>	Two-striped garter snake		X	
Colubridae	<i>Thamnophis sirtalis</i>	San Francisco garter snake			X
Crotaphytidae	<i>Crotaphytus bicinctores</i>	Great Basin collared lizard			X
Crotaphytidae	<i>Gambelia copeii</i>	Long-nosed leopard lizard		X	X
Emydidae	<i>Clemmys marmorata</i>	Pacific pond turtle	IUCN-V		X
Phrynosomatidae	<i>Holbrookia propinqua</i>	Keeled earless lizard		X	
Phrynosomatidae	<i>Petrosaurus mearnsi</i>	Banded rock lizard		X	
Phrynosomatidae	<i>Sceloporus occidentalis</i>	Western fence lizard			X
Phrynosomatidae	<i>Sceloporus orcutti</i>	Granite spiny lizard		X	
Phrynosomatidae	<i>Sceloporus vanderburgianus</i>	Southern sagebrush lizard		X	
Phrynosomatidae	<i>Uma notata</i>	Colorado Desert Fringe-toed lizard		X	
Phrynosomatidae	<i>Urosaurus nigricaudus</i>	Baja California brush lizard		X	X
Scincidae	<i>Eumeces skiltonianus</i>	Western skink			X
Teiidae	<i>Aspidoscelis laredoensis</i>	Laredo striped whiptail		X	
Teiidae	<i>Aspidoscelis sexlineata</i>	Six-lined racerunner			X
Viperidae	<i>Sistrurus catenatus</i>	Massasauga			X
Xantusiidae	<i>Xantusia henshawi</i>	Henshaw's night lizard		X	
<i>Mammals</i>					
Cricetidae	<i>Oryzomys couesi</i>	Coues's rice rat			X
Cricetidae	<i>Peromyscus fraterculus</i>	Northern Baja deer mouse		X	
Felidae	<i>Puma yagouaroundi</i>	Jaguarundi	US-E, MX-T		X
Heteromyidae	<i>Chaetodipus californicus</i>	California pocket mouse			X
Heteromyidae	<i>Chaetodipus fallax</i>	San Diego pocket mouse		X	
Heteromyidae	<i>Chaetodipus rudinoris</i>	Baja pocket mouse			X
Heteromyidae	<i>Chaetodipus spinatus</i>	Spiny pocket mouse		X	
Heteromyidae	<i>Dipodomys simulans</i>	Dulzura kangaroo rat		X	

Table 2 Continued.

Family	Species	English names	IUCN or binational threatened and border barrier > 50% of range	Larger subrange < 10 ⁵ (km ²) and border barrier > 50% of range	Range margin and border barrier > 50% of range
Heteromyidae	<i>Liomys irroratus</i>	Mexican spiny pocket mouse			X
Sciuridae	<i>Sciurus arizonensis</i>	Arizona gray squirrel		X	
Sciuridae	<i>Sciurus griseus</i>	Western gray squirrel			X
Sciuridae	<i>Tamias merriami</i>	Merriam's chipmunk		X	X
Sciuridae	<i>Tamias obscurus</i>	California chipmunk		X	
Soricidae	<i>Sorex monticolus</i>	Dusky Shrew			X

Species were considered at risk from current barriers if they (1) had a larger national subrange < 10⁵ km² (risk G2), (2) were near range margins at the border (risk L1, ratio of distances from border to range edges < 0.15) or (3) were classified as threatened by the IUCN or both nations (risk G1), and over 50% of their border range is occupied by current barriers (i.e. length of barriers in range/length of border in range > 0.5). Richness of these species along the border is shown in the dashed lines of Fig. 4. E, endangered; V, vulnerable; T, threatened.

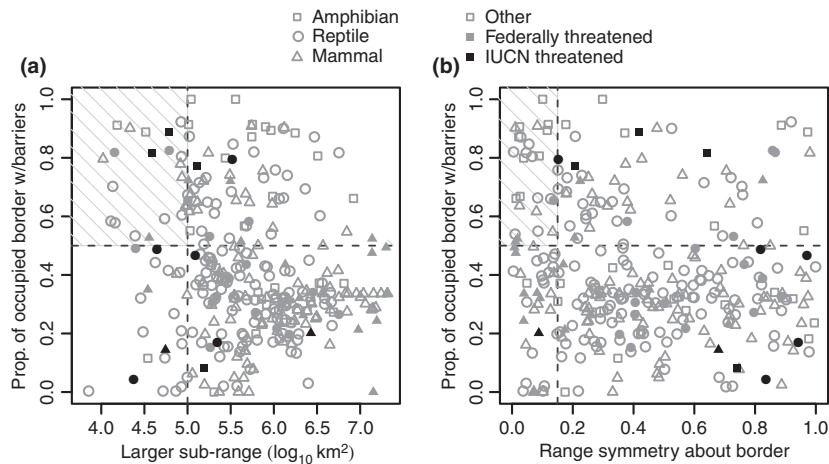


Figure 6 Identification of vulnerable species based on extent of barriers within the range and range area and symmetry. The proportion of species' border ranges occupied by barriers is plotted against (a) the area of the larger national subrange and (b) the symmetry of the range about the border as measured with the ratio of distances from border to range edges. Species approaching the border near their range limit will have a high degree of asymmetry in subranges and equivalently a small ratio of the distance between the border and the edge of one subrange relative to the larger subrange. We identify species to the left of the dashed lines as risk (a) globally or (b) locally because of potential extensive future barriers (G2 & L1). Species above the dashed line in the shaded regions are considered most at risk from current barriers. The species in the shaded regions are listed in Table 2, and spatial patterns of their richness are documented in Table 1 and Fig. 2. Squares-amphibians, circles-reptiles and triangles-mammals. Filled characters represent threatened species: black-IUCN threatened, grey- federally threatened in at least one nation.

indicate where dispersal barriers could affect the greatest number of species and where barriers along the entire border would bisect the greatest number of species ranges (Fig. 3).

Spatial variation in regional species richness, composition and risk might be explained by regional environmental variation. Species range limits are often coincident with sharp environmental gradients, and the orientation of gradients affects the risk posed by barriers along the border. In North America, mountain ranges are oriented along a north-south axis leading to a similar north-south orientation of small species ranges for terrestrial vertebrates (Brown & Maurer,

1989). This pattern is repeated in the California, Madrean and Gulf ecoregions, which are narrow along the border and bounded on either side by sharp gradients. The border in these regions passes nearly perpendicular to contours of equal environmental conditions, and as a result, barriers have a high potential to bisect species ranges. In contrast, the Chihuahuan Desert is larger and extends far along the border. Thus, the assemblages of the Chihuahuan Desert had relatively low complementarity, fewer small range size species and fewer species with large portions of their range occupied by current barriers.

The coastal California ecoregion, which was the narrowest ecoregion, is bounded by the two steepest environmental gradients on the border a short distance apart: to the west, the Pacific Ocean, and to the east, the border's steepest drop in mean annual precipitation (National Atlas, 2008). This region coincided with a peak in complementarity and had the most species at risk globally because of potential isolation into small subranges (Purvis *et al.*, 2000). This region was also richest in endemic species with small total range size, although the peak of species with small subranges in this region was more pronounced. A caveat to range size metrics is that they might be biased towards higher threat estimations for small-bodied species. Given equal population size between two species (and thus equal risk from inbreeding and stochastic extinction, all else being equal), one large-bodied and one small, we would estimate greater risk for small-bodied species because their range sizes tend to be smaller (Brown *et al.*, 1996). Nevertheless, range size remains a widely used criterion for assessing species risk (IUCN, 2008).

Peaks in the regional species richness of mammals and reptiles were associated with steep elevation and precipitation gradients and coincident heterogeneity in dominant vegetation physiognomy (Sayre & Knight, 2010). For amphibians, peak diversity was associated with the highest mean annual precipitation along the border (National Atlas, 2008). This distinct pattern of amphibian diversity may have contributed to the high complementarity of Gulf Coast assemblages. Regions of highly diverse border fauna extended hundreds of kilometres away from the border in some regions, and thus drivers of border ecosystem change (e.g. extensive dispersal barriers) might affect ecosystems across a large transborder area (Lopez-Hoffman *et al.*, 2010). While regions of greatest overall species richness along the border include areas with peaks in officially threatened species, they do not include the coastal areas of highest complementarity and rich in species most at risk under other criteria (Ceballos & Ehrlich, 2006).

The species we identified as being globally at risk because of small subrange size were generally different than range margin species locally at risk (Table 2). Although these represent two distinct targets of conservation efforts, they coincided spatially in the California border region. Accordingly, previous researchers have prioritized the California border region for global and national conservation and the Madrean archipelago and Gulf coastal plain for national conservation (Dobson *et al.*, 1997; Myers *et al.*, 2000; Koleff *et al.*, 2007; Riemann, 2007).

The species we identified as most at risk from current barriers represent a first list of candidates for studying the impacts of barriers along the border. The richness of these species peaks in the coastal regions. On the west coast, the California border is the location of the metropolitan area of San Diego/Tijuana and many border fences. On the Gulf coast, the Rio Grande Valley currently has extensive fencing, high urbanization and intensive agriculture that have reduced cover of native thorn forest to < 5% (Harveson *et al.*, 2004). Pedestrian fences and highly disturbed landscapes complement each other as barriers in these regions.

Estimates of the intersection of species ranges with barriers may be inaccurate because some barriers are shorter than the scale at which range maps are reliable. For two reasons, we believe this error would introduce negligible, if any, bias and would not alter the general patterns we observed. First, analyses of species range areas and range margins, irrespective of barriers, show the same three regions to be home to species with small ranges or at range margins. Secondly, given that these regions are characterized by small or marginal species ranges and contain many barriers, it follows that barriers in these regions threaten to bisect ranges.

We emphasize that dispersal barriers need not be completely impermeable to have significant effects on populations (Levins, 1970; With *et al.*, 1997; Keitt *et al.*, 2001; Epps *et al.*, 2005). If the populations of species near range margins at the US–Mexico border are maintained by cross-border dispersal, as authors have suggested, limiting their dispersal could greatly increase the risk of extirpation in one nation (Cohn, 2007; List, 2007; Spangle, 2007; Varas, 2007; McCain & Childs, 2008; Flesch *et al.*, 2010). Marginal populations can be important to species' genetic diversity and may be important to future species' evolution, especially against a background of environmental change (Lesica & Allendorf, 1995). Dispersal may also play a key role in community assembly (MacArthur & Wilson, 1967; Hubbell, 2001; Leibold *et al.*, 2004), so that barriers may also alter ecological communities.

We have likely omitted some species meriting closer attention because of the limited species-level data available to estimate risk. Our analyses likely overlooked barriers that may divide populations of vulnerable subspecies (List, 2007; Flesch *et al.*, 2010). Barriers along the border may also impede dispersal of volant animals (Trombulak & Frissell, 2000; List, 2007; Drewitt & Langston, 2008; Flesch *et al.*, 2010). While our metric of assessing risk through small total range and subrange size was likely biased towards small-bodied animals, we identified federally threatened large mammals of local conservation interest (e.g. *Ursus americanus*) as range margin species at risk. The large-bodied, federally threatened, jaguar (*Panthera onca*) was omitted from the species potentially at risk that we identified, as little information exists on its current range in the United States. However, jaguars' range apparently crosses the border in the Madrean Archipelago region (McCain & Childs, 2008), which we identified as an important region for preserving transborder connectivity.

The biota of North America has a long history of range shifts associated with environmental changes (Webb & Bartlein, 1992). Currently, many species are shifting their ranges polewards in association with global climate change (Parmesan, 2006). This expansion may be necessary for species persistence to offset range contraction on southern range edges. However, reduced permeability of the US–Mexico border might slow the dispersal-limited process of climate-space tracking (Willis *et al.*, 2009) or halt species' range expansion (Keitt *et al.*, 2001). A less permeable southern border may reduce species' ability to colonize suitable environments in the southern United States.

Future studies should use demographic and tracking data from species indicated herein to precisely locate key populations and dispersal routes (e.g. McCain & Childs, 2008; Flesch *et al.*, 2010). Researchers should study species' propensity to cross-border dispersal barriers (e.g. Flesch *et al.*, 2010). Researchers could then make more informed determinations of whether existing or proposed barriers would put species and populations at risk of extinction. Additionally, exploration of the life history characteristics associated with vulnerability to border barriers could suggest specific mechanisms behind negative impacts on species.

Mitigation and future of border dispersal barriers

Barriers may have the effect of restricting the cross-border movement of animals to unfenced portions (McCain & Childs, 2008). Animals may be funnelled to such crossings by maintaining natural vegetation around openings in barriers (Cain *et al.*, 2003), although such funnelling would increase distance (and thus energetic cost) of cross-border dispersal. Restriction of dispersal to bottlenecks may increase the chance that localized environmental disturbances divide populations. Vegetative cover that allows dispersing animals to obscure themselves conflicts with a goal of US CBP: maintaining visibility of human border crossers (US DHS, 2008b). CBP plans to spray herbicide along the Rio Grande to eradicate the invasive reed *Arundo donax* (US DHS, 2008a). Although this action may have positive effects on native biodiversity, it highlights conflicting goals of law enforcement and dispersing wildlife.

The activity of humans in unfenced areas may also restrict animal dispersal, such that border permeability may be significantly reduced in areas we did not identify as barriers. Areas of high human activity probably do not occur randomly with respect to barriers. Rather, rural areas left unfenced will become bottlenecks for undocumented human traffic and law enforcement, which disturb soil, vegetation and animals (Cohn, 2007; Romo, 2007; Spangle, 2007; McCain & Childs, 2008). Bottlenecking of traffic may exacerbate the problem of human activity by concentrating human activity that was previously dispersed across a larger area. Reductions in illegal traffic because of fencing, however, could have the benefit of reducing disturbance in adjacent areas. Whether this outweighs the negative impacts of fencing requires study. Barriers that limit the dispersal of both humans and animals could lead to humans and animals competing for use of unfenced borderlands, which is an asymmetric contest favouring humans.

Mitigation in the priority regions should increase border permeability. Decreasing the anthropogenic impact in unfenced regions and increasing the size and frequency of openings in fences and walls may promote transborder dispersal (Moya, 2007). The richness of species with large portions of their range occupied by current barriers indicates locations where new barriers could bisect ranges of species already in jeopardy (dashed lines, Fig. 5). When planning for additional fences, walls and land use change along the border, the combined effects of all barriers should be a primary consideration. The

utility of mitigation actions will be improved by conservation efforts beyond the immediate border regions.

Pedestrian barriers might pose a more immediate threat to border conservation than land use change because of the rapid speed with which pedestrian barriers have been constructed (~ 800 km in ~ 2 years; Government Accountability Office, 2009). Future border policy of the US government is difficult to predict, although there may be further dramatic increases in barriers. The original legislation expanding fences (although later amended, US Government Printing Office, 2008) mandated installation of pedestrian fencing across nearly the entire Arizona border and lower Rio Grande Valley (USLOC, 2006). In recent years, legislation has been introduced in the US Congress to expand the current level of pedestrian fences (US House of Representatives Committee on Rules, 2009) and to fence the entire US–Mexico border (USLOC, 2005a). Lower-level governments may also build barriers; the Arizona State Senate has recently passed legislation authorizing construction of pedestrian fences (Arizona State Legislature 2011). President Barack Obama (then a legislator) supported the 2006 law that dramatically expanded border barriers, although the Obama administration has not yet signalled interest in expanding border fences further (Yellin, 2009). However, in the past year, prominent Republican legislators (who control the House of Representatives) have called for constructing additional fences (Goldman, 2010). The Obama administration has been pursuing immigration reform that would be linked to heightened border security (Yellin, 2009), possibly by means of physical barriers (USLOC, 2010).

Under the REAL ID Act of 2005, the Secretary of the DHS has authority to fence the entire border at any time without the oversight of environmental regulatory law that regulates all other infrastructure projects (USLOC, 2005b). This lack of oversight is detrimental to biodiversity conservation efforts and increases the importance of further research on the impacts of barriers along international borders. The REAL ID Act should be amended to reinstate environmental regulation of border security efforts.

CONCLUSIONS

This is the first transcontinental study, to our knowledge, to quantitatively evaluate potential impacts of dispersal barriers on the highly biodiverse ecological communities along the US–Mexico border and the first to provide planning recommendations based on such an analysis. Notably, the border fauna of the California, Madrean Archipelago and Gulf Coast regions merit attention for further research and conservation of transborder connectivity. Further monitoring and environmental protection are recommended for the border region, which is subject to rapid and uncontrolled anthropogenic transformations.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Figure S1 Complementarity of local assemblages along the border.

Appendix S1 Locations of border fence and wall.

Appendix S2 Categories describing composition of border fences and walls.

Appendix S3 Amphibian, reptile, and mammal species of the border.

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BIOSKETCHES

Jesse Lasky is a graduate student who studies the spatial distribution of biodiversity.

Walter Jetz is a professor who is interested in the way environment, evolutionary history and chance affect ecological patterns at the level of the individual and combine to form patterns at the scale of continents or the whole globe.

Tim Keitt is a professor currently studying scale-specific inference using wavelets and estimation and analysis of spatial network models.

Author contributions: J.R.L., W.J. and T.H.K. contributed equally to this work.

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