APPLIED ISSUES

Effects of coupled natural and anthropogenic factors on the community structure of diadromous fish and shrimp species in tropical island streams

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SUMMARY

1. Overlapping river and road networks provide a framework for studying the complex interactions between natural and human systems, with river-road intersections as focal areas of study. Roads can alter the morphology of stream channels, pose barriers to freshwater fauna, provide easy access to streams for humans and non-native species and accelerate the expansion of urban development.

2. We determined what variables control the structure of diadromous fish and shrimp communities and assessed whether particular road crossings altered community structure in north-eastern Puerto Rico. We identified 24 sites that represented a range of river and road sizes across two catchments that drain El Yunque National Forest in Puerto Rico.

3. The location of natural barriers and the size of stream pools were the most important variables for predicting six of fifteen fish and shrimp distributions. Predatory fishes were predicted to be limited to areas in the river network below large, steep waterfalls, whereas adult shrimp *Atya lanipes* (Atyidae) were predicted to be present above these waterfalls. The fish *Awaous banana* was predicted to be present in pools >11.6 m wide, whereas the shrimp *Xiphocaris elongata* was predicted to be present in pools <10.4 m wide. The distributions of nine species were predicted poorly, but three of these species were common and three were rare.

4. Although urban and agricultural land covers were among the top three predictors of five species distributions, they were probably good predictors because they were correlated with the natural gradient. Further study is necessary to disentangle natural and anthropogenic gradients.

5. Road crossings, 10 of which were culverts, were not dispersal barriers for fishes or shrimps. On average, species were present both upstream and downstream from road crossings at 68% of sites where they occurred. Absences upstream or downstream from road crossings occurred at 16% of sites each and likely resulted from a failure to detect species.

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6. Several existing features of these catchments and taxa may aid in fish and shrimp conservation. The headwaters are protected by management practices of El Yunque National Forest, connectivity within the river network has been maintained, and the diadromous life history of these organisms makes them resilient to pulsed disturbances.

Introduction

Linking natural and human systems within a common framework for environmental analysis requires an interdisciplinary approach (Colwell, 1998; Michener *et al.*, 2001; Pickett, Cadenasso & Grove, 2005; Liu *et al.*, 2007; Forman, 2008). Overlapping river and road networks provide a meaningful template under which the physical, biological and social elements of the landscape may be integrated. The road network is a conduit for the dispersal of people, providing easy access to rivers and guiding development as human populations expand outward from urban centres (Forman, Sperling & Bissonette, 2003). Similarly, migratory fauna navigate through river networks, and materials such as sediments, organic material and nutrients are transported downstream. We employed an analysis of river and road networks in Puerto Rico to conceptualise how the movement of people and the species they rely on for supplying essential ecosystem goods and services interact. The intersections of these networks are focal areas for study compared with similar aquatic habitats lacking road access.

Direct connections between river and road networks have been widely studied in relation to physical and biological components of streams. Roads increase surface run-off, creating a more variable hydrograph and increasing sedimentation rates (Trombulak & Frissell, 2000; MacDonald, Sampson & Anderson, 2001). Roads are associated with agricultural and urban development, which cause increased sedimentation, increased concentrations of nutrients and pollutants and decreased species diversity (Weaver & Garman, 1994). Roads act as conduits for anglers and invasive species and focus the impacts of recreational uses of rivers (Trombulak & Frissell, 2000). Culverts can act as barriers to movement of stream fauna (Trombulak & Frissell, 2000; Resh, 2005; Norman *et al.*, 2009).

Diadromous fauna may be especially sensitive to road building and other forms of development if connectivity between the ocean and headwater streams is not maintained. Unlike ''habitat patches'' in terrestrial systems, which may be colonised via many pathways, a single barrier in a river network may isolate an entire catchment from the rest of the basin (Fagan, 2002). Species naturally confined to highly disturbed streams at low altitudes may suffer reduced abundances (McDowall, 2007). Species that spend the majority of their life cycle in headwater streams may also be impacted if anthropogenic barriers impede or severely reduce migration (Benstead *et al.*, 1999; Blanco & Scatena, 2007). Despite the large body of work documenting effects of roads on streams (Trombulak & Frissell, 2000), few studies have been conducted in the tropics (but see MacDonald *et al.*, 2001; Blanco & Scatena, 2005).

The island of Puerto Rico provides an excellent location to study the interactions between humans and the environment among intersecting river and road networks. Nearly all of the non-insect, stream fauna have a diadromous life cycle and migrate through a dense river network over steep terrain (Blanco & Scatena, 2006, 2007; Kikkert, Crowl & Covich, 2009). At 438 people per km^2, Puerto Rico also has one of the highest population densities on the planet (U.S. Census Bureau, 2007). Extensive road building has occurred, with high road densities in catchments of north-eastern Puerto Rico. Although El Yunque National Forest protects the headwaters of nine catchments from urban and agricultural development, logging and fishing, the extent and intensity of urban development continues to expand outside forest boundaries (López, Aide & Thomlinson, 2001; Lugo *et al.*, 2004). Densely clustered human populations also result in high demands on water resources. Approximately 70% of the water draining El Yunque National Forest is diverted into municipal water supplies before reaching the ocean (Crook, Scatena & Pringle, 2007).

Our goal in this study was to determine what factors structure diadromous fish and shrimp

communities in two catchments in north-eastern Puerto Rico. We used a variety of variables representing natural (e.g. waterfalls, pool morphology, streambed grain size) and anthropogenic (e.g. urban and agricultural land covers, fine sediments) features of the landscape to predict individual species distributions. We used non-metric multidimensional scaling (NMDS) to look for patterns in fish and shrimp community structure. We expected species absences from reaches at low altitudes if urban and agricultural land covers altered habitat and water quality downstream.

To assess direct effects of roads on fish and shrimp distributions, we compared species occurrence patterns immediately upstream and downstream from road crossings. If culverts acted as physical barriers, we expected species absences to occur upstream from road crossings. Culverts should be greater barriers to fishes and shrimps than bridges. If road crossings altered downstream habitat, we expected taxa to be absent immediately downstream from individual road crossings. We expected greater effects at sites with road crossings (culverts or bridges) than sites without (trails alongside the stream). Sampling efficiency might cause absences from pools downstream or upstream from individual road crossings, but not in a consistent pattern.

Methods

Study area and fauna

From June to August 2005, we sampled two catchments that drain the steep terrain of the Luquillo Experimental Forest, an 11 000-ha reserve in north-eastern Puerto Rico also known as El Yunque National Forest, and previously as the Caribbean National Forest (18°18′N, 65°47′W). Both the Espíritu Santo and Mameyes Rivers are steeply sloped drainages and drop *c.* 950 m in altitude over a 16–19 km distance to the ocean (Pike, 2008; Pike, Scatena & Wohl, 2010; Fig. 1). Headwater stream flow is highly variable and responds rapidly to rainfall, which averages 3600 mm per year (Covich, Crowl & Heartsill-Scalley, 2006). The mean annual discharge of the two catchments is similar: 1.7 m^3 s^{-1} in the Espíritu Santo [U.S. Geological Survey (USGS) station number 50063800, gauged drainage area 22.3 km^2, period of record 1994–2002] and 1.5 m^3 s^{-1} in the Mameyes (50065500, 17.8 km^2, 1991–2004). The peak discharge recorded at each of
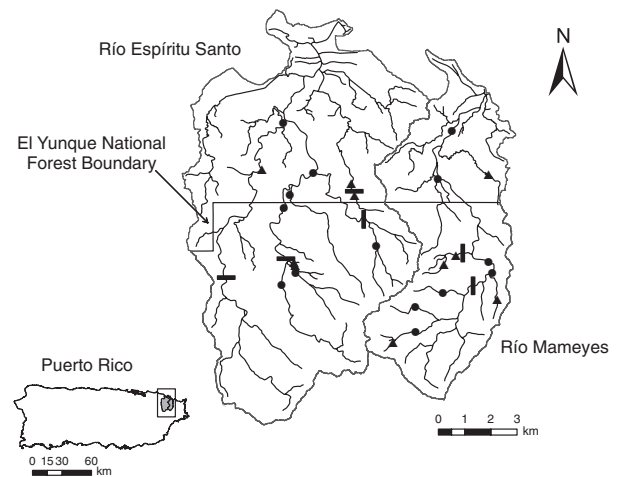

Fig. 1 Map of study sites (filled circles or filled triangles for road crossings that used culverts) in the Espíritu Santo and Mameyes catchments, which drain El Yunque National Forest in north-eastern Puerto Rico. The – symbol indicates the downstream-most waterfalls (average slope of 35%).

these gauge stations was 600 m^3 s^{-1} in the Espíritu Santo (1966–2004) and 580 m^3 s^{-1} in the Mameyes (1969–2003; http://nwis.waterdata.usgs.gov/nwis).

Six species of native, diadromous freshwater fishes reside in these catchments: mountain mullet (*Agonostomus monticola* Bancroft), bigmouth sleeper (*Gobiomorus dormitor* Lacépède), smallscaled spinycheek sleeper (*Eleotris perniger* Cope), American eel (*Anguilla rostrata* LeSueur), river goby (*Awaous banana* Valenciennes) and sirajo goby (*Sicydium plumieri* Bloch). Previous studies referred to *Eleotris pisonis* (Gmelin) in Puerto Rico, but a recent study shows that *E. pisonis* occurs only in South America and *E. perniger* occurs in the Caribbean (Pezold & Cage, 2002). Watson (1996) identified *A. banana* as a distinct species from *Awaous tajasica* (Lichtenstein) and recently split *S. plumieri* into four different species (Watson, 2000). All fishes are predators of shrimps and other taxa except the sirajo goby, which consumes algae and other plant material (Erdman, 1986). Most native fishes are catadromous, spending their adult life in rivers and migrating to the estuary for breeding and larval development. Both gobies and all shrimp species are amphidromous: they spend adulthood in the headwaters and their larvae get washed to the estuaries (Covich & McDowell, 1996). Exotic fishes are rare in these catchments, with few Mozambique tilapia (*Oreochromis mossambicus* Peters) in the estuary of the Espíritu Santo (Smith, Corujo Flores & Pringle, 2008)

and three guppies (*Poecilia* spp.) at one high-altitude site. Five species of atyid and xiphocarid shrimp live in these streams: *Atya lanipes* (Holthuis), *Atya innocuous* (Herbst), *Atya scabra* (Leach), *Micratya poeyi* (Guérin-Méneville) and *Xiphocaris elongata* (Guérin-Méneville). *Xiphocaris elongata* are mainly detritivores (Crowl *et al.*, 2001, 2006); *Atya* spp. have modified chelae that they use to filter feed and scrape algae (Covich & McDowell, 1996). Five species of predatory palaemonid shrimp inhabit these streams: *Macrobrachium carcinus* (Linnaeus), *Macrobrachium crenulatum* (Hothuis), *Macrobrachium heterochirus* (Wiegmann), *Macrobrachium faustinum* (de Saussure) and *Macrobrachium acanthurus* (Wiegmann). *Macrobrachium* spp. have large chelae and consume shrimp, crabs, aquatic insects, molluscs, small fish, algae, macrophytes and decomposing leaf litter (Crowl & Covich, 1994; Covich & McDowell, 1996).

Biotic sampling

In 2005, we sampled 24 sites within the Espíritu Santo and Mameyes catchments associated with road/trail networks (Fig. 1). Four sites were associated with hiking trails, one site was contiguous with a road, and the remaining sites were at river-road crossings that represented a range of combinations of road and stream sizes. Ten river-road crossings were culverts, whereas nine river-road crossings were pylon-bridge structures that had free flowing water beneath. At each site, we sampled at least three and usually four pools (two upstream and two downstream from the road) for a total of 88 pools across all study sites.

We used a combination of snorkelling, electrofishing and trapping to sample the fishes and shrimps in each pool. When water was clear, two people snorkelled pools deep enough to swim (>0.5 m). Two people used a Smith-Root model 12-B battery-powered electrofisher (Vancouver, WA, U.S.A.) to sample pools and adjacent riffles in a single pass moving upstream. Because large pools were too deep to electrofish, adjacent riffles provided the most complete fish species occurrence data. We used three types of traps to sample all pools at all sites: wire-mesh Gee minnow traps (Cuba Specialty Mfg. Co., Inc., Fillmore, NY, U.S.A.) with a 3-cm-diameter opening, modified Gee minnow traps with a 5-cm-diameter opening and large cylindrical traps (35 cm diameter, 65 cm long) with a 13-cm-diameter opening. We scaled trap effort to pool size with one of each type of trap set in small pools (<30 m^2), three of

each type of minnow trap and two large traps set in medium pools (30–200 m^2) and five of each type of minnow trap and two large traps set in large pools (>200 m^2). Each trap was baited with 22 g of chicken and fish-based dry pellets (cat food) and set over night. Larger traps were used because they are better suited for capturing large *Macrobrachium* spp. observed to occur in all sizes of pools.

Because of the range in sampling methods and sampling intensity across stream sizes, our analyses focused on species presence–absence (incidence functions) rather than relative abundance. We modelled the presence and absence of 15 shrimp and fish species across both catchments. *Micratya poeyi* were smaller than the mesh size of our traps and dip nets and were not included in the analysis. To further reduce the likelihood of incorrectly classifying a species as absent, we aggregated the three to four pools sampled at a site to model species distributions.

Predictor variables

We used a geographic information system (GIS) to generate a suite of variables for each site where we sampled fishes and shrimps (Table 1). We used hydrographic data (USGS Digital Line Graphs, attributes correspond to USGS National Mapping Program Standards), land cover data (Gónzalez Ramos, 2001) and a 10-m-resolution digital elevation model (DEM; Pike, 2008) to calculate a number of natural and anthropogenic features of the landscape that might affect community structure. As a proxy for

Table 1 Potential predictor variables used in the random forest modelling

Predictor variable	Median value	Range of values
Derived from GIS		
Maximum slope*	35%	1–90%
Urban (upstream catchment)	0.1%	0–17%
Agriculture (upstream catchment)	0%	0–76%
Derived from geomorphic field surveys		
Base flow channel width	7.1 m	2.2–22.3 m
Coefficient of variation of depth	0.36	0.21–0.65
Median grain size (d50)	132 mm	13–1327 mm
Bedrock	7%	0–53%
Cobble	21%	6–40%
Fine sediment	0.1%	0–40%

GIS, geographic information system.
*See definition in Methods section.

waterfalls, we used the DEM to calculate the greatest change in altitude over a 10-m distance downstream from each site (Pike, 2008). Although direct measurements of waterfall height were available in some areas (Pike, 2008), the DEM calculation was more generally applicable to other catchments. These geomorphic features are referred to as ''maximum slope.'' We calculated the land cover (per cent urban, agricultural or forest) within the upstream catchment area. Variables derived from field surveys provided measures of pool morphology and substrata (Table 1; Pike, 2008). We averaged the pool morphology and grain size variables across pools within each site.

The predictor variables were highly correlated with one another. The steep gradient of these catchments constrained the geomorphic properties of the stream channel and the spatial arrangement of land development. The slope of the channel increased rapidly at *c.* 12–14 km inland (Pike, 2008; Pike *et al.*, 2010). With this increase in slope, streambed grain size increased and pool lengths and widths decreased (Pike, 2008; Pike *et al.*, 2010). Urban and agricultural development was primarily limited to lower altitudes below the boundaries of El Yunque National Forest. The mean altitudes of urban, agricultural and protected forest lands within these catchments were 53, 63 and 486 m a.s.l., respectively.

To reduce collinearity among the predictors, we selected a subset of variables that represented landscape position, anthropogenic stressors, pool size and grain size. Pearson correlation coefficients (ρ) were calculated between predictor variables to select variables that were not highly correlated with one another. Among the nine selected variables (Table 1), nine of thirty-six correlations were significant ($P < 0.05$). Five of these significant correlations had correlation coefficients >0.5. Maximum slope was negatively correlated with urban land cover ($\rho = -0.66$) and positively correlated with median grain size ($\rho = 0.52$). Urban and agricultural land covers were positively correlated ($\rho = 0.56$) and per cent fine sediments increased with agricultural land cover ($\rho = 0.82$). Median grain size was positively correlated with per cent bedrock ($\rho = 0.58$).

Statistical analyses

To predict species distributions, we used both random forests and classification trees because they make no

assumptions about data distributions or the shape of response relationships (De'ath & Fabricius, 2000; Guisan & Zimmermann, 2000; Breiman, 2001), and they often outperform more traditional approaches (Olden & Jackson, 2002; Cutler *et al.*, 2007). Random forests are a collection of hundreds of classification trees, with each tree based on a bootstrap sample of the data and each split of the tree offered a subset of the predictors (Breiman, 2001). Each tree gives one vote using the remaining observations (those not used in the training data set), and the collection of votes gives the forest class prediction for an individual observation. We used a 50% vote of the models in the forest to determine presence or absence. Unlike classification trees, random forests cannot be over-fit and are especially useful when there are few sample sites and many possible predictors (Breiman, 2001). However, ecological interpretation of random forest models is more difficult than that of a single classification tree. The importance of individual predictor variables is ranked using various indices (Breiman, 2002), with the most important variables closer to the tree roots. However, the combinations of tree splits and the break point values of individual predictors are not specified as in classification trees.

We used the randomForest library (Liaw & Wiener, 2002) in the R statistical package (R Development Core Team, 2007) to develop individual species distribution models and then examined the variable importance plots of moderate to high performing models. We used four metrics to assess model performance: (i) per cent of presences correctly classified (sensitivity), (ii) per cent of absences correctly classified (specificity), (iii) per cent of all observations correctly classified (PCC) and (iv) Cohen's kappa, which corrects for chance when measuring agreement between predicted and actual class assignments (Manel, Williams & Ormerod, 2001; Cutler *et al.*, 2007). Because species prevalence influences the values of the first three metrics but not the fourth (Manel *et al.*, 2001; Olden, Jackson & Peres-Neto, 2002), we used κ to evaluate model performance, retaining moderate (0.4–0.6) to very high (0.8–1.0) performing models for further analysis (Manel *et al.*, 2001). We used the Gini index of variable importance for our analyses (Breiman, 2002; Cutler *et al.*, 2007), with higher values indicating greater importance. To understand how the single most important variable influenced each species distribution, we created classification trees for the

six species with moderate to high performing random forest models. We used the tree library (Ripley, 1996) in the R package to carry out the classification tree analyses (Breiman *et al.*, 1984). Because secondary splits did not improve prediction (the same class was predicted at both leaves), we pruned all trees to one split.

To understand how the fish and shrimp community structure varied across sites, we ordinated all species presence/absence data with NMDS in PC-ORD (McCune & Mefford, 1997). We used the Sorenson distance matrix. Two pairs of sites had the exact same community assemblage, so the distances between these pairs of sites were zero. We eliminated one of these sites from analysis because NMDS does not allow null values in the distance matrix. We chose NMDS over other ordination approaches because it does not assume linear relationships, uses rank distances and is generally recommended for analyses on ecological communities (McCune & Grace, 2002).

We analysed species occurrence patterns at the pool level to examine direct effects of road crossings. We did not analyse road effects at the site level because natural barriers excluded some species from high-altitude sites. We used ANOVA to test the effects of road type (culvert, bridge or trail) on the per cent of sites where a species was absent from all upstream pools. Species served as replicates ($n = 11$), and

percentages were calculated among the sites where the species occurred. For example, *X. elongata* was absent from all upstream pools at one of nine (11%) culvert sites where they occurred. *Eleotris perniger*, *A. innocuous*, *A. scabra* and *M. acanthurus* were not included in the analysis because they were completely absent from at least one of the three road types. We performed a second ANOVA on the per cent of sites where a species was absent from all downstream pools. We used PROC GLM in SAS (version 9.1; SAS Institute, Cary, NC, U.S.A.) to fit the models.

Results

Incidence functions

Six of fifteen species distribution models performed moderately to very well, with κ values ≥ 0.5 and more than 79% of observations correctly classified (Table 2). The maximum downstream slope was most important for predicting distributions of *A. lanipes* and the fishes *A. rostrata*, *A. monticola* and *G. dormitor* (Fig. 2). *Atya lanipes* was predicted present at high altitudes above waterfalls, whereas the predatory fishes were predicted present below these points in the river network (Table 3). These four species shared the same threshold in maximum slope, which was 35% (Table 3). Base flow pool width was the most

Table 2 Accuracy measures for fish and shrimp species presence/absence random forest models. There were a total of 24 sites.

Species	Presences	Sensitivity	Specificity	PCC	κ
*Atya lanipes**	11	90.9	100.0	95.8	0.915
Anguilla rostrata	13	92.3	90.9	91.7	0.832
Agonostomus monticola	13	92.3	90.9	91.7	0.832
Gobiomorus dormitor	10	80.0	78.6	79.2	0.577
Awaous banana	8	62.5	87.5	79.2	0.516
*Xiphocaris elongata**	18	94.4	50.0	83.3	0.500
Sicydium plumieri	17	82.4	42.9	70.8	0.263
*Atya innocuous**	11	72.7	53.8	62.5	0.260
Eleotris perniger	4	25.0	95.0	83.3	0.250
*Macrobrachium crenulatum**	10	60.0	64.3	62.5	0.239
*Atya scabra**	2	0.0	100.0	91.7	0.000
*Macrobrachium acanthurus**	3	0.0	100.0	87.5	0.000
*Macrobrachium heterochirus**	9	33.3	66.7	54.2	0.000
*Macrobrachium carcinus**	20	90.0	0.0	75.0	−0.125
*Macrobrachium faustinum**	20	90.0	0.0	75.0	−0.125

*Denotes a shrimp species.
Model 'sensitivity' is the per cent of presences correctly classified, 'specificity' is the per cent of absences correctly classified, 'PCC' is the overall per cent of observations correctly classified, and 'κ' is a measure of agreement between predicted and actual class assignments that corrects for chance.
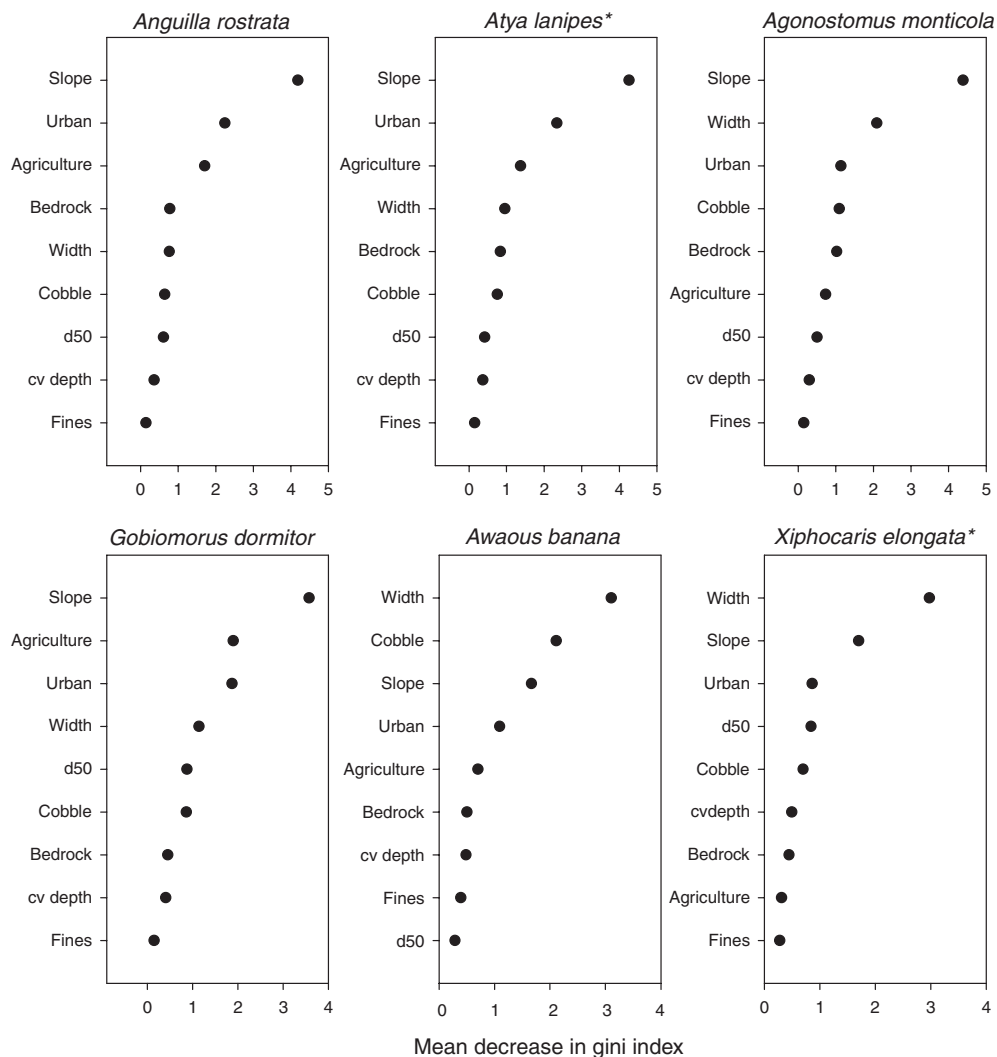
Fig. 2 Variable importance plots of the four fish and two shrimp (*) species whose random forest models of presence⁄absence were robust ($\kappa \geq 0.5$). Note that axes are not constant across plots.

Table 3 Classification trees built using the most important predictor variable as determined by random forest models (see Fig. 2). Classification trees were only built for those species whose random forest models performed moderately to very well ($\kappa \geq 0.5$)

Species	Split	Sens	Spec	PCC	κ	κ^2
*Atya lanipes**	Slope ≥ 35%	100.0	92.3	95.8	0.917	0.75
Anguilla rostrata	Slope < 35%	92.3	100.0	95.8	0.917	0.75
Agonostomus monticola	Slope < 35%	92.3	100.0	95.8	0.917	0.67
Gobiomorus dormitor	Slope < 35%	100.0	85.7	91.7	0.833	0.74
Awaous banana	Pool width > 11.6	75.0	100.0	91.7	0.800	0.69
*Xiphocaris elongata**	Pool width < 10.4	88.9	100.0	91.7	0.800	0.56

*Denotes a shrimp species.

The split indicates the conditions necessary for the species to be present. 'Sens' refers to the sensitivity of the model (per cent of presences correctly classified), 'Spec' is the specificity of the model (per cent of absences correctly classified), 'PCC' is the overall per cent of observations correctly classified, and 'κ' is a measure of agreement between predicted and actual class assignments that corrects for chance. For comparison, 'κ^2' gives the κ value that results when the second most important predictor identified by the random forests was used by the classification tree.

important predictor for the distributions of one shrimp and one fish species (Fig. 2). *Xiphocaris elongata* was predicted to be present in pools <10.4 m wide, whereas *A. banana* was predicted present in pools larger than 11.6 m wide (Table 3). Classification trees that used the second most important variables identified by random forests did not perform as well as those that used the most important variables; κ values decreased by 0.09–0.24 (Table 3).

Urban and/or agricultural land covers were among the three most important variables predicting five species distributions (Fig. 2). We hypothesised that some species of fishes and shrimps would be absent at sites downstream from urban and agricultural lands, but classification tree models based on a single land-cover-variable predicted the fishes *A. rostrata*, *A. monticola* and *G. dormitor* to be present at sites downstream from catchments composed of more than 0.05–0.8% urban land cover or 2–4.8% agricultural land cover. Models of *A. lanipes'* distribution did fit our expectation, with this shrimp species predicted to be absent at sites with more than 0.8% urban or 2% agricultural land cover upstream. Both urban and agricultural land covers decreased with increasing altitude ($\rho = -0.60$ and -0.52, respectively). Most natural barriers were near the boundaries of El Yunque National Forest (Fig. 1). Therefore, break points near 0% urban or agricultural land in upstream catchments corresponded well with the location of waterfalls.

Nine of fifteen species distribution models performed poorly, with κ values <0.27 (Table 2). Three species (*M. carcinus*, *M. faustinum* and *S. plumieri*) were common in the landscape and the ability to predict absence was low, whereas three species (*M. acanthurus*, *A. scabra* and *E. perniger*) were rare, and the ability to predict presence was low (Table 2). *Atya innocuous*, *M. crenulatum* and *M. heterochirus* were moderately prevalent, but still the power to predict these species distributions across the landscape was low.

Community composition

The most striking pattern in fish and shrimp community structure across the landscape was the distinction between sites with and without predatory fishes (Fig. 3). Shrimp species richness was higher at sites without predatory fishes (mean of 6.6 species
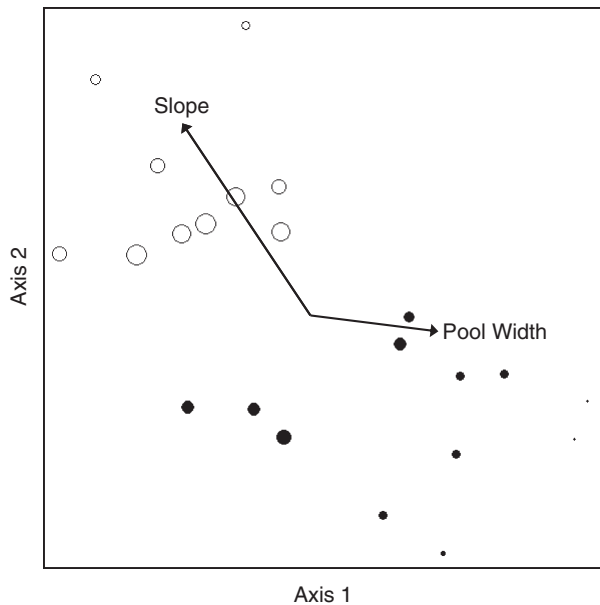

Fig. 3 Non-metric multidimensional scaling plot of all sites in the Espíritu Santo and Mameyes catchments. Each point represents the assemblage of fish and shrimp species at a site. Larger points indicate greater shrimp species richness, and the shading of the points indicates the presence (black) or absence (white) of predatory fishes (*G. dormitor*, *A. monticola*, *A. rostrata*, *A. banana* or *E. perniger*). Vectors represent the correlations of two environmental variables with the ordination; vector length is proportional to the strength of the interaction.

compared to 3.5 species, *post-hoc t*-test, $P < 0.001$). The vector representing the location of waterfalls (maximum slope) pointed towards the upper left corner of the ordination, perpendicular to the break between sites with and without predatory fishes. This pattern also shows that predatory fishes were absent at steep gradient, high-altitude sites above waterfalls, whereas shrimp were present at these sites (Figs 3 & 4). All predatory fishes abruptly dropped out of the stream community at *c.* 12 km from the ocean, which was within the range of distances (9–14 km) where the stream gradient rapidly increases (Fig. 4). Most predatory fishes were limited to altitudes below 270 m a.s.l., but *A. monticola* were observed at one site 380 m a.s.l. The only herbivorous fish (*S. plumieri*) was present at sites ranging from the highest to lowest altitudes (Fig. 4). Below barriers to predatory fishes, decapod species richness declined with increasing pool width (Fig. 3). Only *M. carcinus* or *M. faustinum* were present at the two sites with the widest pools to the far right of the plot (Fig. 3).
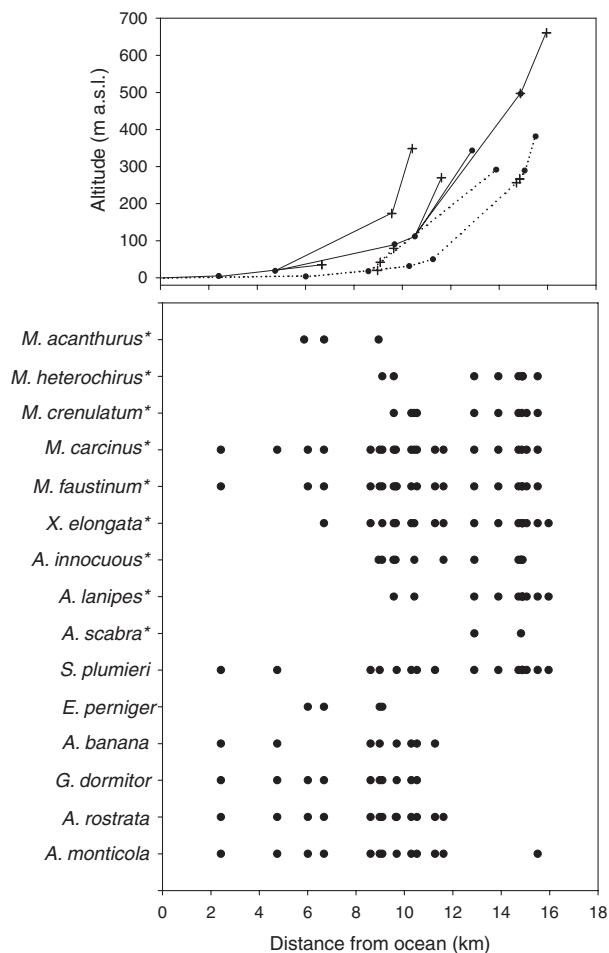
Fig. 4 Distributions of fish and shrimp (*) species in relation to the altitudinal gradient. The upper plot shows the altitude and distance from the ocean of each site. Lines in the upper plot depict the connectivity of sites in the Mameyes (solid) and Espíritu Santo (dotted) catchments. Sites include trails and bridges (filled circles) and culverts (+). The filled circles in the lower plot depict the sites where each species was present.
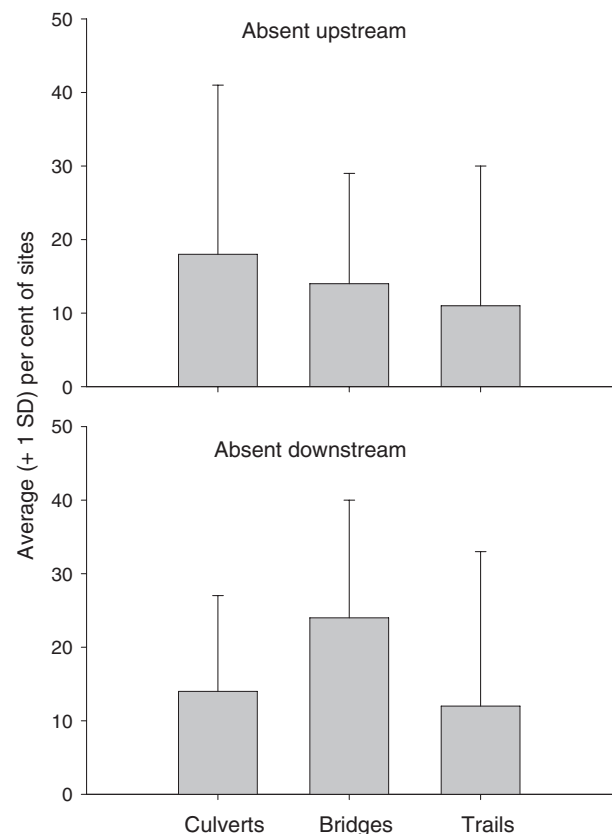

Fig. 5 Average (+1 standard deviation) per cent of sites where species were absent from: (i) all pools upstream from the road crossing or (ii) all pools downstream from the road crossing. Averages were calculated across species at sites that used culverts (n = 10), bridges (n = 9) or trails (n = 5).

Direct effects of road crossings

Fish and shrimp distributions did not differ immediately upstream or downstream from road crossings. On average, species were present both upstream and downstream from road crossings at 68% of sites where they occurred (standard deviation = 20%). Species were absent from all upstream pools at an average of 16% (SD = 13%) of sites and were absent from all downstream pools at an average of 16% (SD = 11%) of sites. There was no effect of road type on the proportion of sites with absences upstream (one-way ANOVA, n = 33, d.f. = 2, 30, F = 0.43,

P = 0.66) or on the proportion of sites with absences downstream (one-way ANOVA, n = 33, d.f. = 2, 30, F = 1.67, P = 0.21; Fig. 5). Furthermore, no single species was consistently found only upstream or only downstream from road crossings.

Because fish distributions are naturally limited by steep slopes, few culverts were accessible to fish. Only four of ten culverts among our sites were downstream from waterfalls (Figs 1 & 4; sites at altitudes <100 m a.s.l.), and the stream slopes at these sites ranged from 0.1 to 6.1%. Among fishes that only occurred downstream from waterfalls, four upstream absences occurred at culverts. These absences represented three species and two sites and did not consistently target a single species or culvert. The remaining six culverts were upstream from natural barriers (stream slopes ranging from 5.8 to 30%) and did not pose permanent barriers to shrimps or to *S. plumieri*. Shrimp species

that were present in pools downstream from the culvert were also present in pools upstream from the culvert at all six sites.

Discussion

In high-gradient river networks dominated by diadromous fauna, the location of natural barriers (i.e. waterfalls) is critical for understanding patterns in community structure. For example, fish communities in New Zealand and Hawaiian rivers, which are dominated by diadromous species, are best explained by the location of barriers and the swimming or climbing ability of individual taxa (Hayes, Leathwick & Hanchet, 1989; McDowall, 1998; McDowall, 2007). Like fishes in many other systems (Townsend & Crowl, 1991; Gilliam, Fraser & Alkins-Koo, 1993; Power & Dietrich, 2002), the ranges of three predatory fishes in Puerto Rico were limited to stream reaches below waterfalls. Our models indicated that a 35% maximum slope (based on a 10-m DEM) best predicted these species' distributions. Although this GIS-derived proxy for waterfall location performed well, *A. monticola* and *A. rostrata* were each found at one site above a 35% maximum slope, indicating that one must know the specific structure of steeply sloped channels to accurately locate all natural barriers. Unlike the three predatory fishes discussed, one goby (*S. plumieri*) and nearly all shrimps can surmount waterfalls. *Sicydium plumieri* has modified pelvic fins that form a suction cup and allow this gobiid fish to climb vertical cliffs (Erdman, 1986).

By excluding predatory fishes, waterfalls may provide upstream refugia to freshwater shrimps. Waterfalls can limit the dispersal of predators and competitors and provide refuge for poor competitor and prey species (Townsend & Crowl, 1991; Feminella & Hawkins, 1994; Brasher *et al.*, 2006). Released from their competitors and/or predators, organisms that have the ability to access these headwater reaches should be much more abundant than they are downstream (Power & Dietrich, 2002; Creed, 2006). We observed this pattern in Puerto Rico, with greater shrimp species richness above waterfalls. Higher *A. lanipes* abundance in fishless streams also occurs in streams within the Espíritu Santo and Mameyes catchments that have been monitored since 1987 (Covich *et al.*, 2009). Shrimps may avoid fish predation by migrating above barriers to fish dispersal

(Hein & Crowl, 2010) and by altering their morphology where fish are present (*sensu* Townsend & Crowl, 1991; Godin & McDonough, 2003).

Urban and agricultural land covers were among the most important predictors of fish and shrimp distributions but were probably good predictors because they were correlated with the natural gradient. First, the hypothesis that dispersal barriers to predatory fishes provide upstream refugia for shrimp offers a mechanistic explanation for understanding largely disparate fish and *A. lanipes* distributions (Covich *et al.*, 2009; Hein & Crowl, 2010). Second, we examined sites where the location of the forest boundary did not exactly match that of barriers to fish dispersal. Fishes were present at three forested sites below barriers. If these fishes were only present in streams altered by human activities, we would not expect them to be present at high-altitude sites within El Yunque National Forest. If *A. lanipes* were not influenced by the distribution of predatory fishes, then they should have been present at the three forested sites below barriers. A survey of more sites with urban or agricultural land above natural barriers and sites with forested land below natural barriers would help disentangle correlated natural and anthropogenic gradients.

The majority of river-road crossings in the Espíritu Santo and Mameyes catchments were not dispersal barriers for diadromous fishes and shrimps. At each site, a few species were present in pools only upstream or only downstream from the road crossing, but this pattern likely reflects a low probability of observing each species in all four pools on one sampling occasion. Nine of nineteen road crossings studied were pylon-bridge structures with free flowing water beneath. Most culverts were above natural barriers to fishes and did not impede dispersal of freshwater shrimps or *S. plumieri*. These organisms have evolved to climb over steep waterfalls (Erdman, 1986; Covich, 2006) and can also climb through culverts. Still, atyid and palaemonid shrimps are unable to surmount a culvert in French Polynesia with a >60 cm drop from the pipe to the stream substrate (Resh, 2005). Culverts often limit dispersal of fishes (Trombulak & Frissell, 2000; Norman *et al.*, 2009) but do not necessarily alter fish community structure (Vander Pluym, Eggleston & Levine, 2008). In our study, most fish species were present up and downstream from the four culverts that were

downstream from natural barriers, but some culverts might restrict the movement of individuals, especially during periods of low flow. More research on the movement patterns of tagged individuals is necessary.

We were unable to fit good models to nine species distributions, but three of these species were abundant and widespread (*M. carcinus*, *M. faustinum*, *S. plumieri*). *Macrobrachium crenulatum* and *M. heterochirus* were present in the upper halves of the two catchments, except for the highest altitude site. Similarly, *A. innocuous* was more commonly found at higher altitude sites. A more specific habitat model might better predict these three shrimp distributions. *Atya scabra* was only sampled at two high-altitude sites in the Mameyes catchment. *Eleotris perniger* and *M. acanthurus* were only present at three to four sites below 40 m a.s.l., and these species are generally limited to stream reaches near the coast (Chace & Hobbs, 1969; Bussing, 1998).

Although we cannot compare current fish and shrimp distributions with historical distributions, the Espíritu Santo and Mameyes appear to be relatively healthy river systems in terms of water quantity and quality (Santos-Román, Warner & Scatena, 2003; Ortiz-Zayas *et al.*, 2005). Compared with other catchments with high head dams, few exotic species have been introduced and abundant, native taxa inhabit the Espíritu Santo and Mameyes catchments (Holmquist, Schmidt-Gengenbach & Yoshioka, 1998; Blanco & Scatena, 2006; Greathouse *et al.*, 2006; Neal, Lilyestrom & Kwak, 2009). Still, the levels of urban development in the Espíritu Santo (21%) and Mameyes (18%) catchments (based on land cover data from Gónzalez Ramos, 2001) were higher than levels of development (6–15%) in other locations worldwide where urbanisation has been associated with declines in the abundance and diversity of stream organisms (Paul & Meyer, 2001; Riley *et al.*, 2005; Alexandre, Esteves & de Morua e Mello, 2010).

The shrimp and fish species in Puerto Rico are adapted to an environment with steep terrain and a high natural disturbance regime. These characteristics allow for (i) recolonisation after pulsed human disturbances (Greathouse, March & Pringle, 2005; Cook *et al.*, 2009; Ramírez *et al.*, 2009) and (ii) the ability to surmount culverts and dams (those with spill water and by-pass structures). Furthermore, most culverts that could pose barriers to fishes (except the sirajo goby) in the two study catchments occurred upstream from natural barriers. Thus, if urban growth is planned carefully to avoid fragmenting river corridors, diadromous fauna may still be conserved. On islands where surface waters provide the only freshwater resources, conserving the habitats and organisms that provide clean water is especially important. The Espíritu Santo and Mameyes Rivers provide an example where recreational and rural economic development can occur while maintaining native diversity, and in turn, the ecosystem processes they influence.

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(Manuscript accepted 27 October 2010)