

# Cross-Cordillera exchange mediated by the Panama Canal increased the species richness of local freshwater fish assemblages

Scott A. Smith<sup>1,3\*</sup>, Graham Bell<sup>1,2</sup> and Eldredge Bermingham<sup>1,3</sup>

<sup>1</sup>Department of Biology, McGill University, and <sup>2</sup>Redpath Museum, 1205 Avenue Doctor Penfield, Montreal, Quebec, H3A 1B1, Canada

<sup>3</sup>Smithsonian Tropical Research Institute, Unit 0948, APO AA 34002-0948, USA

Completion of the Panama Canal in 1914 breached the continental divide and set into motion a natural experiment of unprecedented magnitude by bringing previously isolated freshwater fish communities into contact. The construction of a freshwater corridor connecting evolutionarily isolated communities in Pacific and Caribbean watersheds dramatically increased the rate of dispersal, without directly affecting species interactions. Here, we report that a large fraction of species have been able to establish themselves on the other side of the continental divide, whereas no species have become extinct, leading to a local increase in species richness. Our results suggest that communities are not saturated and that competitive exclusion does not occur over the time-scale previously envisioned. Moreover, the results of this unintentional experiment demonstrate that community composition and species richness were regulated by the regional process of dispersal, rather than by local processes such as competition and predation.

**Keywords:** saturation; local and regional processes; competitive exclusion; species richness; biological invasions; biotic interchange

## 1. INTRODUCTION

Patterns in natural communities have often been studied to understand the ecological mechanisms underlying them. One extreme view is that communities are closely fitted to the landscapes that they inhabit, each species occupying a distinctive niche and contributing an essential element to overall community function. The extinction of any species is likely to impair community processes, and invasion is unlikely because communities are already 'saturated' with well-adapted species. However, if invasion occurs it will be disruptive and it is likely to cause the extinction of one or more resident species. The opposite view is that communities are loosely organized, with most species not precisely adapted to the sites that they occupy. Extinction of a species will seldom have any substantial effect at the community level and invasion is commonplace but will not necessarily, or often, cause the extinction of resident species. Two manifestations of these opposing points of view are the clash between neutralist and functionalist interpretations of community properties, and the debate concerning local and regional effects on species richness.

Contrasting predictions regarding the invasibility and saturation of local communities arise because of the failure of ecologists to reconcile the scales over which local and regional processes act (Ricklefs 2004). The belief that ecological communities become saturated and subsequently resistant to invasion, as well as the idea that local and regional processes operate on different time-scales have greatly hindered the development of community ecology (Ricklefs 2004). The question of whether local communi-

ties are saturated has troubled ecologists for the past 20 years (Terborgh & Faaborg 1980; Ricklefs 1987, 2004; Cornell & Lawton 1992; Srivastava 1999; Bell 2003). Evidence regarding the state of saturation of local communities arising from local–regional richness plots (Srivastava 1999), biotic interchanges (Vermeij 1991) and biological invasions (Case 1996; Gido & Brown 1999; Sax *et al.* 2002) suggests that communities are not ecologically saturated with species. Clear, definitive evidence that local communities are not saturated, however, has thus far eluded the grasp of ecologists because of methodological issues concerning the use of local–regional richness plots as tests of community saturation (Srivastava 1999; Shurin & Srivastava 2004), in addition to the vagaries of the fossil record and the large spatial scales over which the outcome of biotic interchanges and biological invasions are recorded. Furthermore, evidence supporting the idea that communities are unsaturated is not unequivocal (Shurin 2000).

The idea that local processes come to equilibrium rapidly compared with evolutionary processes is entrenched in the mind-set of many ecologists (Ricklefs 1989, 2004). Studies of the processes regulating community structure have been conducted over short time-scales and have relied on microcosm experiments with discrete boundaries and simplified structure (Ricklefs 2004). These studies have led to the conclusion that competitive exclusion occurs in local communities on the time-scale of 10–100 generations (Ricklefs 1989), a much shorter time-scale than that which species production and other evolutionary processes are thought to occur ( $10^5$  years or more; Magallon & Sanderson 2001; Ricklefs 2003). This observation, as well as the belief that local communities are saturated, led to the

\* Author for correspondence (ssmith3@po-box.mcgill.ca).

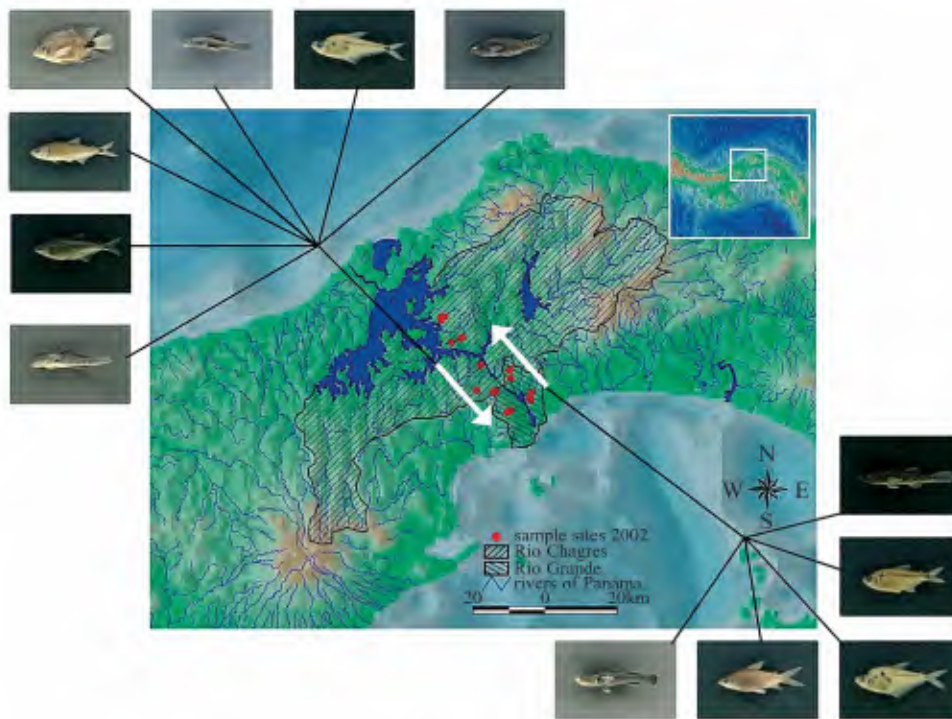


Figure 1. The Panama Canal experiment. The Panama Canal is represented by the narrow body of water traversing the Isthmus from the Pacific to the Caribbean, and passing through the man-made Lake Gatun. Species that colonized the Rio Grande from the Rio Chagres are depicted in the top left (moving up and to the right, they are *Sicydium altum*, *Brycon chagrensis*, *B. petrosus*, *Vieja maculicauda*, *Ancistrus chagresi*, *Roeboides guatemalensis* and *Dormitator maculatus*) and species that colonized the Rio Chagres from the Rio Grande are situated in the bottom right-hand corner (moving down and to the left, they are *Gobiomorus maculatus*, *Astyanax aeneus*, *R. occidentalis*, *Cyphocharax magdalenae* and *Eleotris picta*).

conclusion that local deterministic processes regulate patterns of local diversity. Empirical evidence, derived from direct evaluation of the relative importance of deterministic, local, selection-driven processes and stochastic, regional, dispersal-driven processes in shaping the attributes of natural communities is required to discern between these competing paradigms. Natural experiments, where the dynamic balance between local and regional processes is disturbed, and the change in local species richness over time is documented (Ricklefs & Schluter 1993; Caley & Schluter 1997), provide a powerful means for testing such hypotheses.

Completion of the Panama Canal in 1914 created a freshwater corridor between the Rio Chagres on the Caribbean slope and the Rio Grande on the Pacific slope of the Isthmus of Panama, enabling the freshwater fish communities occupying the hitherto isolated drainage basins to intermingle (figure 1). Although the Central American continental divide is relatively low in the region of the Panama Canal, it was nonetheless an effective barrier to the dispersal of freshwater fishes before the construction of the canal (Meek & Hildebrand 1916). Indeed, biogeographic analyses suggest that the Rio Chagres and the Rio Grande are members of discrete ichthyological provinces (S. A. Smith and E. Bermingham, unpublished data). Breaching of the continental divide allowed increased fish dispersal between drainages, without directly altering species interactions. Thus, the natural experiment that was initiated with the flooding of the Panama Canal offers a rare opportunity to test whether dispersal-driven or

selection-driven processes governed the attributes of fish assemblages in the rivers of the Panama Canal watershed.

Here, we document the outcome of the biotic interchange that occurred after the completion of the Panama Canal separately for communities of obligate (primary and secondary) freshwater and peripheral fishes. Myers (1949) established categories of freshwater fishes based on the salinity tolerance of these fishes, which he inferred from the fishes' geographical distribution. Primary and secondary freshwater fishes live in freshwater streams and rivers, and their dispersal is dependent on direct connections between water bodies (Myers 1938, 1966; Loftin 1965; Miller 1966; Bermingham & Martin 1998; Unmack 2001). Peripheral fishes often inhabit estuarine habitats and can disperse along the coastline; however, they are physiologically and ecologically adapted to living either all or a portion of their life in freshwater habitats (Miller 1966; Myers 1966; Bussing 1976; Winemiller & Ponwith 1998; Nordlie 2000). We use this unintentional natural experiment to test whether local communities are saturated and to determine if competitive exclusion is an important process setting the upper limit to the number of species coexisting in ecological communities.

## 2. MATERIAL AND METHODS

S. E. Meek and S. F. Hildebrand, ichthyologists associated with the Smithsonian Biological Survey of the Panama Canal Zone, conducted a survey of the freshwater and peripheral fishes in the Rio Grande and Rio Chagres between January 1911 and March 1912 (Meek & Hildebrand 1916). They visited approximately 22 sites in the Rio Chagres and 10 sites in the Rio Grande during



their ichthyological survey of the Canal Zone, and used seine nets and ichthyocides to sample the fish fauna. These collections, completed before the breach of the continental divide, provide the historical baseline for comparison of changes in the species richness of the fish assemblages of the Rio Chagres and the Rio Grande.

We collected freshwater and peripheral fishes in streams and tributaries of both the Rio Chagres and the Rio Grande drainage basins during the dry season between 7 February and 11 April 2002. During the quantitative portion of our survey, we visited a total of seven sites in the Rio Grande and eight sites in the Rio Chagres. At each site, a stream reach of 150 m was sampled. Block nets were placed at the bottom and the top of the stream reach to prevent fish migration in or out of the sampling area. Two passes per stream reach were conducted using both a backpack electroshocker and seine nets. At a few sites, we conducted a third pass per stream reach and caught very few individuals (data not presented), suggesting that our sampling procedure captured the vast majority of fishes within the sampled area. To supplement the quantitative portion of our survey, we visited two other sites in the Rio Pedro Miguel and one in the Rio Cardenas, using an adapted version of our quantitative sampling procedure. Moreover, we used the Smithsonian Tropical Research Institute (STRI) 'neotropical freshwater fish collection' and its associated database to complement our collecting efforts (Bermingham *et al.* 1997). This database contained 628 records in the Rio Chagres, divided into 35 species and 31 genera, and 192 records in the Rio Grande, divided into 22 species and 19 genera prior to our survey.

All of the sites that were sampled in our survey were situated in relatively pristine tropical forest, except for one site in the Rio Cardenas that was sampled qualitatively. In the Rio Chagres watershed, we did not sample below lake-level because the creation of Lake Gatun following the flooding of the Panama Canal created a new habitat that might have facilitated invasion into this part of the watershed. Furthermore, the introduction of *Cichla ocellaris*, a voracious predatory fish native to the Amazon River, into Lake Gatun in 1967 devastated the shoreline fish assemblage of the lake (Zaret & Paine 1973), which may have opened up ecological space facilitating invasion of other prey species. The geographical distribution of *C. ocellaris* within the Panama Canal watershed is largely confined to lacustrine habitats; *C. ocellaris* was not captured above lake-level during our survey, or more generally, during 15 years of sampling the streams of the Rio Chagres watershed (Bermingham *et al.* 1997). Other ichthyologists have not found *C. ocellaris* in the tributaries of the Rio Chagres (S. A. Smith and E. Bermingham, unpublished data). It is therefore very likely that the influence of *C. ocellaris* is confined to Lake Gatun, and does not extend into the rivers where we collected our samples.

To standardize our experiment to the historical baseline, we considered only those species determined to inhabit the Rio Chagres and the Rio Grande by Meek & Hildebrand (1916) and Hildebrand (1938) (table 1). Our contemporary survey of fishes from the streams and tributaries draining into the Panama Canal watershed enabled us to document cross-divide colonization events, and determine whether or not local extirpation had occurred in the fish communities of the Rio Grande and the Rio Chagres.

Furthermore, our quantitative survey permitted us to evaluate the relative success of invaders in terms of the number of sites occupied by colonists and the relative abundance that colonists achieved within the local assemblages (Gaston 1994). Occupancy success of colonists was calculated by dividing the percentage of occupancy (or the number of sites occupied/number of sites in the survey) of colonists in their native habitat by that in the newly invaded drainage. Similarly, abundance success was calculated by

dividing the percentage of the total abundance of each colonist in their native drainages by that in the invaded drainage. Nested ANOVA analyses were used to determine whether invaders were significantly more abundant in their native versus their invaded drainage basins. Species abundances were log transformed prior to analyses to normalize the data.

### 3. RESULTS

Our survey, complemented by the collections recorded in the STRI database, provides a reference point from which to evaluate the efficiency of Meek & Hildebrand's (1916) pre-Canal survey of the freshwater fishes of the Rio Chagres and the Rio Grande. Comparisons between our survey and that of Meek & Hildebrand (1916) attest to the efficiency of their description of the freshwater fish fauna of the Rio Chagres and the Rio Grande (see table 2 in electronic Appendix A). Most of the species that appear in our collections but are absent from Meek & Hildebrand's (1916) collections were exclusively collected at sites in the upper reaches of the Rio Chagres drainage basin that Meek and Hildebrand did not visit. Others were extremely rare in our collections; for example, during our exhaustive survey of the Rio Grande, we only ever collected one specimen of *Priapichthys dariensis*.

Many species were able to disperse through the Canal and establish themselves on the other side of the divide (figure 1). Colonization events following completion of the Panama Canal were rapid. Hildebrand (1938) surveyed the post-Canal watershed and documented that *Astyanax aeneus*, *Brycon chagrensis*, *B. petrosus* and *Vieja maculicauda* had already established cross-divide populations by 1937. In total, three fish species colonized the Rio Chagres from the Rio Grande, and five species colonized the Rio Grande from the Rio Chagres (table 1). We have not been able to identify any characters that differ consistently between species that did and did not succeed in crossing the divide. For example, both trophic generalists (*B. chagrensis* and *A. aeneus*) and trophic specialists (*Roebooides occidentalis* and *R. guatemalensis*) successfully participated in cross-divide colonization events (see table 3 in electronic Appendix A). Moreover, a large percentage of the regional species pool was able to participate in the faunal interchange. Colonists represented 75% and 38.5% of the total number of species that were potentially able to colonize the Rio Chagres from the Rio Grande (and vice versa) and which had not already done so prior to the construction of the Panama Canal. If, however, we adopt a less conservative approach and consider the assemblage of freshwater fishes not limited to those species initially collected by Meek & Hildebrand (1916), but whose geographical range (Bermingham *et al.* 1997) suggests that these fishes might represent post-Canal additions to the Rio Chagres and the Rio Grande, we document the addition of two more species of freshwater fishes in the Rio Chagres (*Imparaes panamensis* and *V. tuyenensis*) and one additional species in the Rio Grande (*B. obscurus*; see table 2 in electronic Appendix A). In subsequent analyses presented herein, we will consider only our conservative estimate of cross-Cordillera colonists.

Our results suggest that no species has been locally extirpated as a consequence of the cross-divide movement of freshwater fishes through the Panama Canal. Consequently, species richness increased by 11% in the Rio

Table 1. The obligate freshwater and peripheral fish assemblages of the Rio Grande and Rio Chagres drainage basins sampled by both Meek &amp; Hildebrand (1916) and the present study.

(Colonists are denoted in bold text and 'new' refers to drainages colonized after completion of the Panama Canal. The species in table 1 are organized by their salinity tolerance, and then by alphabetical order of family, genus and species names. A nested ANOVA analysis of species log-transformed abundances in adjacent watersheds was performed to determine whether species were more successful in their native or newly colonized drainages. \* are values significant at  $p = 0.05$  and \*\* are values significant at  $p = 0.01$ , and the location of the symbol indicates whether the species was more successful in its native or recently invaded drainage.)

	Rio Grande	Rio Chagres
Primary and secondary freshwater fishes		
<b><i>Astyanax aeneus</i></b>	+	new
<i>Astyanax ruberrimus</i>	+	+
<b><i>Brycon chagrensis</i></b>	new	+
<b><i>Brycon petrosus</i></b>	new	+
<i>Bryconamericus emperador</i>	+	+
<i>Compsura gorgonae</i>	+	+
<i>Gephyrocharax atricaudata</i>	+	+
<i>Hyphessobrycon panamensis</i>	–	+
<i>Pseudocheirodon affinis</i>	–	+
<b><i>Roeboides occidentalis</i></b>	+*	new
<b><i>Roeboides guatemalensis</i></b>	new	+*
<b><i>Cyphocharax magdalенаe</i></b> <sup>a</sup>	+	new**
<i>Hoplias microlepis</i>	+	+
<i>Piabucina panamensis</i>	+	+
<b><i>Ancistrus chagrensis</i></b>	new	+*
<i>Chaetostoma fischeri</i>	–	+
<i>Hypostomus panamensis</i>	+	+
<i>Rineloricaria uracantha</i>	–	+
<i>Pimelodella chagresi</i>	+	+
<i>Rhamdia quelen</i>	+	+
<b><i>Brachyhyopomus occidentalis</i></b> <sup>b</sup>	+	+
<i>Rivulus brunneus</i>	–	+
<i>Aequidens coeruleopunctatus</i>	+	+
<i>Archocentrus panamensis</i>	–	+
<i>Geophagus crassilabris</i>	–	+
<b><i>Vieja maculicauda</i></b>	new	+
<i>Brachyrhaphis cascajalensis</i>	–	+
<i>Brachyrhaphis episcopi</i>	+	+
<i>Neoheterandria tridentiger</i>	+	+
<i>Poecilia gillii</i>	+	+
<i>Poeciliopsis elongata</i>	+	–
Peripheral fishes		
<i>Dormitator latifrons</i>	+	–
<b><i>Dormitator maculatus</i></b>	new	+
<i>Eleotris amblyopsis</i>	–	+
<b><i>Eleotris picta</i></b>	+	new
<i>Eleotris pisonis</i>	–	+
<i>Gobiomorus dormitator</i>	–	+
<b><i>Gobiomorus maculatus</i></b>	+	new
<i>Awaous banana</i>	–	+
<i>Awaous transandeanus</i>	+	–
<b><i>Sicydium altum</i></b>	new	+
<i>Sicydium salvini</i>	+	–
<i>Leptophilypnus fluviatilis</i>	–	+
<i>Agonostomus monticola</i>	–	+
<i>Joturus pichardi</i>	–	+

<sup>a</sup> *Cyphocharax magdalенаe* was not captured by Meek & Hildebrand (1916); however, the authors captured it in the drainage basins adjacent to the Rio Grande and concluded that it was indeed part of the pre-1914 fauna of the Rio Grande. In addition, the geographical distribution of *Cy. magdalенаe* suggests that this species migrated through the Panama Canal.

<sup>b</sup> *Brachyhyopomus occidentalis* was not captured in the Rio Grande by Meek & Hildebrand (1916), probably owing to both its rarity and the difficulties involved in collecting this fish, and consequently we have not considered this species as a cross-divide colonist.

Chagres, and by 28% in the Rio Grande (or by three and five species, respectively). It is, however, conceivable that competitive exclusion of resident species has occurred at

spatial scales smaller than that of entire drainages. The spatial resolution of the historical data prevents evaluation of this hypothesis. Nevertheless, exclusion or failed invasions

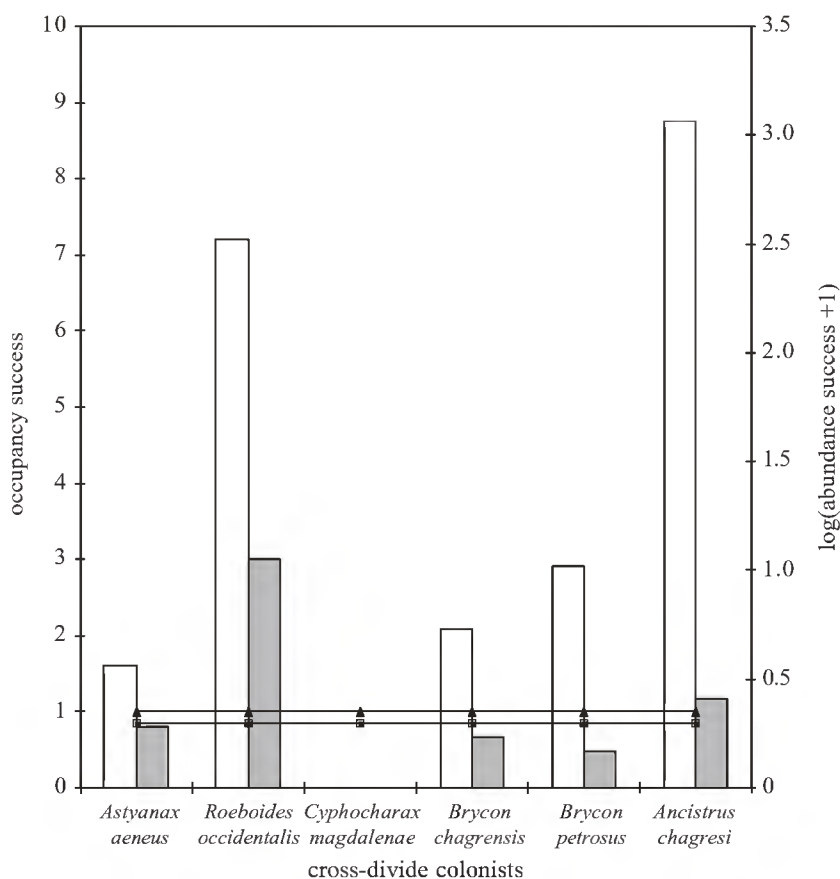


Figure 2. The abundance (grey bars) and occupancy (open bars) success of primary and secondary freshwater fish colonists in the Panama Canal watershed. Only cross-divide colonists for whom we have quantitative data were included in these figures. The horizontal line bisecting the columns represents the value indicating equal abundance (squares), or occupancy (triangles) success in the native and translocated drainage basins.

at very small spatial scales have not led to invasion resistance at larger spatial scales in other systems (Levine 2000; Byers & Noonburg 2003), and our results clearly indicate that the assemblages of freshwater fishes in the Rio Chagres and the Rio Grande were not saturated at the spatial scale of drainage basins.

Cross-divide colonists became common in newly invaded communities, achieving a level of distribution and abundance comparable with their respective abundance in their source communities. One of the six freshwater fish colonists for which we have quantitative information was more successful in its newly invaded range than in its native range in terms of both its relative abundance and the number of occupied sites (figure 2). Several other colonists attained similar quantitative success in both drainage basins (figure 2). Nested ANOVA analyses of species-log transformed abundances in adjacent watersheds indicate that *Cy. magdalenae* was significantly more abundant in its invaded drainage basin, whereas *R. occidentalis*, *Ancistrus chagrensis* and *R. guatemalensis* were significantly more abundant in their native versus their newly invaded drainage basin. For all other species reported in figure 2, there was no statistically significant difference between abundance in native versus invaded drainages.

Patterns of faunal exchange of primary and secondary freshwater fishes across the Isthmus of Panama are mirrored by those of peripheral fishes. Invasions in adjacent communities of peripheral fishes on opposite sides of the

continental divide following completion of the Panama Canal were numerous. Colonists were able to rapidly disperse through the Canal and establish cross-divide populations. Hildebrand (1938) noted that *Dormitator maculatus*, *Eleotris picta* and *Gobiomorus maculatus* participated in cross-divide colonization events prior to 1937. In total, two species of peripheral fishes colonized the Rio Chagres from the Rio Grande and two species of peripheral fishes colonized the Rio Grande from the Rio Chagres (table 1). The colonists represented 40% and 22% of the total number of species that were potentially able to colonize the Rio Chagres from the Rio Grande (and vice versa) and which had not already done so prior to the construction of the Panama Canal. We did not, however, estimate the quantitative success of peripheral fishes because our sampling design was not suitable to do so. In both cases, colonization events did not result in the local extirpation of resident species; therefore net species richness increased by 22% in the Rio Chagres and by 40% in the Rio Grande (or by two species, respectively).

#### 4. DISCUSSION

The outcome of the natural experiment that occurred following the completion of the Panama Canal provides undisputable evidence that local freshwater fish assemblages were not saturated. Our results suggest that local communities of lower Mesoamerican freshwater and peripheral fishes are certainly invasible; 22–75% of the



regional species pool participated in cross-divide colonization events. Moreover, cross-divide colonization events did not result in a single case of local extinction, resulting in net increases in species richness of 11–40%. Contemporary biotic interchanges of fishes across the Isthmus of Panama therefore provide strong evidence that stochastic, dispersal-driven processes play a central role in determining community structure.

Vermeij (1991) and Ricklefs & Schluter (1993) predicted that faunal exchanges should be asymmetrical, with invaders from the more species-rich region achieving greater colonization success because they have evolved superior defences against predators and diseases (Brown 1957; Warner 1968; Ricklefs & Cox 1972; Van Riper *et al.* 1986). We have identified similar numbers of successful invaders in each direction, however, in spite of the fact that the pre-Canal Chagres basin contained nine more species of obligate freshwater fishes and four more peripheral fishes than the Rio Grande. Furthermore, our quantitative assessment of species' colonization success did not indicate that colonists from the more species-rich Rio Chagres were able to achieve greater occupancy success or higher relative abundances in their new drainage basins than colonists from the Rio Grande (figure 2). Thus, the hypothesis that species from species-rich regions are superior competitors is not supported by our results.

In a similar vein, invaders achieved similar occupancy and abundance in both native and newly colonized drainages, suggesting that escape from the effects of natural enemies that have been observed in other systems (Keane & Crawley 2002; Shea & Chesson 2002; Torchin *et al.* 2003) did not influence the success of invasions in the natural experiment of the Panama Canal.

We have documented no cases of local extinction over the 90 year history of the Panama Canal experiment. It is conceivable that the invasion of an exotic species is followed by the extinction of a resident species only after a considerable time lag, and that the Panama Canal experiment has to run for more time to observe local extinctions. Nonetheless, if competitive exclusion is an important process setting limits on the species richness of local communities, our results suggest that it does not occur on the time-scale of 10 to 100 generations. Whether competitive exclusion is truly an important process in setting an upper limit to the number of species that can coexist in local communities is still, however, open to debate. Palaeontological studies of biotic interchanges indicate that species invasions following the elimination of a dispersal barrier rarely cause the extirpation of residents over evolutionary time-scales (Barry *et al.* 1991; Flynn *et al.* 1991; Lindberg 1991).

Local and regional processes might act over completely different time-scales (Ricklefs 1989; Cornell & Lawton 1992), so that the lack of saturation that we have recorded for freshwater fish assemblages of the Panama Canal reflects the relatively young age of the lower Central American freshwater fish fauna. The primary freshwater fish fauna colonized the region following the Pliocene rise of the Isthmus of Panama (Bermingham & Martin 1998), and thus it is possible that there has been insufficient time for the process of speciation to 'saturate' local communities with new species. Thus, the role of dispersal in governing the number of species coexisting in local communities might be exaggerated relative to that of local deterministic

processes. In this event, it would not be possible to evaluate rival ecological controls of species richness in communities that have existed for less than five million years. Phylogeographic analyses of *Anolis* lizards on Caribbean islands, however, demonstrate that after 30 million years of adaptive radiation, the species richness of local communities is still increasing and remains below the speciation–extinction equilibrium (Losos & Schluter 2000). Speciation may be so slow relative to environmental change that few communities ever approach evolutionary equilibrium (Losos & Schluter 2000; Ricklefs & Bermingham 2001).

Finally, populations in the invaded drainages recorded in our survey, although large, might be maintained primarily through ongoing immigration from the source populations. However, current evidence indicates that the invaders are self-sustaining in their expanded range. Previous studies of the freshwater fishes of the Panama Canal have documented the extensive use of shoreline habitat in Lake Gatun by riverine species, facilitating dispersal between opposite slope drainage basins (Zaret & Paine 1973). *Cichla ocellaris* devastated the Lake Gatun shoreline assemblage of freshwater fishes after its introduction in 1967, and populations of cross-divide colonists such as *Astyanax*, *Roeboides*, *Eleotris* and *Gobiomorus* were almost completely extirpated (Zaret & Paine 1973). The presence of *C. ocellaris* in Lake Gatun for the past 36 years has probably acted as a secondary barrier to the dispersal of fishes through the Panama Canal, making it unlikely that continued immigration could explain the maintenance of the populations of cross-divide colonists in their newly invaded drainage basins.

The devastating effects of the introduction of *C. ocellaris* on the diversity of freshwater fishes in Lake Gatun (Zaret & Paine 1973) compared with the positive effects of cross-Canal invasions provides a contrasting view of the effects of invasion on resident assemblages. The introduction of exotic species with novel ecological functions has been documented to have large negative effects on naive local assemblages (Kaufman 1992; Nalepa & Schloesser 1993; Fritts & Rodda 1998; Vanderploeg *et al.* 2002). *Cichla ocellaris* is no exception. The success of *C. ocellaris* probably reflects substantial differences between its performance and that of native piscivores. Vermeij (2004) hypothesized that such differences are most likely in island-like environments such as lakes and mountain tops. The global trend of continental habitats becoming increasingly fragmented, and thus more 'island-like', will render species assemblages more vulnerable to biological causes of extinction (Vermeij 2004). By contrast, the invasion of ecologically similar species, at least in the case of the freshwater fishes of the Panama Canal, appears to have a positive effect on species richness. Understanding the mechanisms underlying these opposing outcomes of invasions is essential to our comprehension of the consequences of human-mediated invasions.

## 5. CONCLUSION

Species invasions mediated by human activity are commonplace (Lodge 1993; Moyle & Light 1996; Lovei 1997; Vitousek *et al.* 1997; Cohen & Carlton 1998; Hobbs & Mooney 1998), but while particular examples have been studied intensively it has seldom been possible to

quantitatively evaluate the outcome of the fusion of two comparable communities. The opening of the Panama Canal has provided an unusually convincing test of ecological theory by connecting two adjacent communities of freshwater fishes. The results clearly contradict the view that the fish communities of this region were saturated with species. The communities were not resistant to invasion, nor were they vulnerable to extinction following invasion. Rather the results are consistent with the predominance of regional effects, in which ecological differences between species are largely over-ridden by immigration, and are even consistent with strictly neutral community models, according to which no such differences exist (Bell 2001; Hubbell 2001). The value of this large-scale unintentional experiment is that it provides, for this situation, a clear answer to a question that has long been inconclusively debated. Similar experiments are likely to provide us with the most convincing analysis of ecological mechanisms.

The authors thank Luis Fernando De Leon, Rigoberto Gonzalez, Neilan Kuntz, Andrew Moeser, Gisela Reina and Oris Sanjur for their help in the field. The manuscript benefited from discussions with R. Craig MacLean and from the comments of Daniel Sol and three anonymous reviewers. S.A.S. was supported by a Natural Science and Engineering Research Council PGS A scholarship. Financial and logistical support was provided by the Smithsonian Tropical Research Institute. The Autoridad Nacional del Medio Ambiente (ANAM) and the Autoridad de la Region Interoceanica (ARI) in Panama kindly provided the required collecting and access permits.

## REFERENCES

- Barry, J. C., Morgan, M. E., Winkler, A. J., Flynn, L. J., Lindsay, E. H., Jacobs, L. L. & Pilbeam, D. 1991 Faunal interchange and Miocene terrestrial vertebrates of southern Asia. *Palaeobiology* **17**, 231–245.
- Bell, G. 2001 Neutral macroecology. *Science* **293**, 2413–2418.
- Bell, G. 2003 The interpretation of biological surveys. *Proc. R. Soc. Lond. B* **270**, 2531–2542. (DOI 10.1098/rspb.2003.2550.)
- Bermingham, E. & Martin, A. P. 1998 Comparative mtDNA phylogeography of neotropical freshwater fishes: testing shared history to infer the evolutionary landscape of lower Central America. *Mol. Ecol.* **7**, 499–517.
- Bermingham, E., Branford, H., Martin, A. P. & Aswani, V. 1997 Smithsonian Tropical Research Institute neotropical fish collection. In *Neotropical fish collections* (ed. L. Malabarba), pp. 37–38. Puerto Alegre, Brazil: Museu de Ciencias e Tecnologia, PUCRS.
- Brown Jr, W. L. 1957 Centrifugal speciation. *Q. Rev. Biol.* **32**, 247–277.
- Bussing, W. A. 1976 Geographic distribution of the San Juan ichthyofauna of Central America with remarks on its origin and ecology. In *Investigations of the ichthyofauna of Nicaraguan lakes* (ed. T. B. Thorson), pp. 157–175. Lincoln, NB: University of Nebraska.
- Byers, J. E. & Noonburg, E. G. 2003 Scale dependent effects of biotic resistance to biological invasions. *Ecology* **84**, 1428–1433.
- Caley, M. J. & Schluter, D. 1997 The relationship between local and regional diversity. *Ecology* **78**, 70–80.
- Case, T. J. 1996 Global patterns in the establishment and distribution of exotic birds. *Biol. Conserv.* **78**, 69–96.
- Cohen, A. N. & Carlton, J. T. 1998 Accelerating invasion rate in a highly invaded estuary. *Science* **279**, 555–558.
- Cornell, H. V. & Lawton, J. H. 1992 Species interactions, local and regional processes, and limits to the richness of ecological communities: a theoretical perspective. *J. Anim. Ecol.* **61**, 1–12.
- Flynn, L. J., Tedford, R. H. & Zhanxiang, Q. 1991 Enrichment and stability in the Pliocene mammalian fauna of North China. *Paleobiology* **17**, 246–265.
- Fritts, T. H. & Rodda, G. H. 1998 The role of introduced species in the degradation of island ecosystems: a case history of Guam. *A. Rev. Ecol. Syst.* **29**, 113–140.
- Gaston, K. J. 1994 *Rarity*. London: Chapman & Hall.
- Gido, K. B. & Brown, J. H. 1999 Invasion of North American drainages by alien fish species. *Freshwat. Biol.* **42**, 387–399.
- Hildebrand, S. F. 1938 A new catalogue of the freshwater fishes of Panama. *Field Mus. Nat. Hist. Zool. Series* **22**, 217–359.
- Hobbs, R. J. & Mooney, H. A. 1998 Broadening the extinction debate: population deletions and additions in California and Western Australia. *Conserv. Biol.* **12**, 271–283.
- Hubbell, S. P. 2001 *The unified theory of biodiversity and biogeography*. Princeton University Press.
- Kaufman, L. 1992 Catastrophic change in species-rich freshwater ecosystems: the lessons of Lake Victoria. *Bioscience* **42**, 846–858.
- Keane, R. M. & Crawley, M. J. 2002 Exotic plant invasions and the enemy release hypothesis. *Trends Ecol. Evol.* **17**, 164–170.
- Levine, J. M. 2000 Species diversity and biological invasions: relating local process to community pattern. *Science* **288**, 852–854.
- Lindberg, D. R. 1991 Marine biotic interchange between the Northern and Southern hemispheres. *Paleobiology* **17**, 308–324.
- Lodge, D. M. 1993 Biological invasions: lessons for ecology. *Trends Ecol. Evol.* **8**, 133–137.
- Loftin, H. G. 1965 *The geographical distribution of freshwater fishes in Panama*. Tallahassee, FL: Florida State University.
- Losos, J. B. & Schluter, D. 2000 Analysis of an evolutionary species–area relationship. *Nature* **408**, 847–850.
- Lovei, G. L. 1997 Global change through invasion. *Nature* **388**, 627–628.
- Magallon, S. & Sanderson, M. J. 2001 Absolute diversification rates in angiosperm clades. *Evolution* **55**, 1762–1780.
- Meek, S. E. & Hildebrand, S. F. 1916 The fishes of the fresh waters of Panama. *Field Mus. Nat. Hist. Zool. Series* **10**, 217–374.
- Miller, R. R. 1966 Geographical distribution of Central American freshwater fishes. *Copeia* **4**, 773–802.
- Moyle, P. B. & Light, T. 1996 Biological invasions of freshwater: empirical rules and assembly theory. *Biol. Conserv.* **78**, 149–161.
- Myers, G. S. 1938 Fresh-water fishes and West Indian zoogeography. *A. Rep. Smithsonian Inst.* **1937**, 339–364.
- Myers, G. S. 1949 Salt-tolerance of fresh-water fish groups in relation to zoogeographical problems. *Bijdr. Dierk.* **28**, 315–322.
- Myers, G. S. 1966 Derivation of the freshwater fish fauna of Central America. *Copeia* **4**, 766–773.
- Nalepa, T. F. & Schloesser, D. W. 1993 *Zebra mussels: biology, impacts and control*. Boca Raton, FL: Lewis Publishers.
- Nordlie, F. G. 2000 Patterns of reproduction and development of selected resident teleosts of Florida salt marshes. *Hydrobiologia* **434**, 165–182.
- Ricklefs, R. E. 1987 Community diversity: relative roles of local and regional processes. *Science* **235**, 167–171.
- Ricklefs, R. E. 1989 Speciation and diversity: the integration of local and regional processes. In *Speciation and its consequences* (ed. D. Otte & J. A. Endler), pp. 599–622. Sunderland, MA: Sinauer.

- Ricklefs, R. E. 2003 Global diversification rates of passerine birds. *Proc. R. Soc. Lond. B* **270**, 2285–2291. (DOI 10.1098/rspb.2003.2489.)
- Ricklefs, R. E. 2004 A comprehensive framework for global patterns in biodiversity. *Ecol. Lett.* **7**, 1–15.
- Ricklefs, R. E. & Bermingham, E. 2001 Non-equilibrium diversity dynamics of the Lesser Antillean avifauna. *Science* **294**, 1522–1524.
- Ricklefs, R. E. & Cox, G. W. 1972 Taxon cycles in the West Indian avifauna. *Am. Nat.* **106**, 195–219.
- Ricklefs, R. E. & Schluter, D. 1993 Species diversity: regional and historical influences. In *Species diversity in ecological communities: historical and geographical perspectives* (ed. R. E. Ricklefs & D. Schluter), pp. 350–363. University of Chicago Press.
- Sax, D. F., Gaines, S. D. & Brown, J. H. 2002 Species invasions exceed extinctions on islands worldwide: a comparative study of plants and birds. *Am. Nat.* **160**, 766–783.
- Shea, K. & Chesson, P. 2002 Community ecology theory as a framework for biological invasions. *Trends Ecol. Evol.* **17**, 170–176.
- Shurin, J. B. 2000 Dispersal limitation, invasion resistance, and the structure of pond zooplankton communities. *Ecology* **81**, 3074–3086.
- Shurin, J. B. & Srivastava, D. S. 2004 New perspectives on local and regional diversity: beyond saturation. In *Meta-communities* (ed. M. Holyoak, R. Holt & M. Leibold). (In the press.)
- Srivastava, D. S. 1999 Using local-regional richness plots to test for species saturation: pitfalls and potentials. *J. Anim. Ecol.* **68**, 1–16.
- Terborgh, J. W. & Faaborg, J. 1980 Saturation of bird communities in the West Indies. *Am. Nat.* **116**, 178–195.
- Torchin, M. E., Lafferty, K. D., Dobson, A. P., McKenzie, V. J. & Kuris, A. M. 2003 Introduced species and their missing parasites. *Nature* **421**, 628–630.
- Unmack, P. J. 2001 Biogeography of Australian freshwater fishes. *J. Biogeogr.* **28**, 1053–1089.
- Vanderploeg, H. A., Nalepa, T. F., Jude, D. J., Mills, E. L., Holeck, K. T., Liebig, J. R., Grigorovich, I. A. & Ojaveer, H. 2002 Dispersal and emerging ecological impacts of Ponto-Caspian species in the Laurentian Great Lakes. *Can. J. Fisheries Aquat. Sci.* **59**, 1209–1228.
- Van Riper III, C., Van Riper, S. G., Goff, M. L. & Laird, M. 1986 The epizootiology and ecological significance of malaria in Hawaiian land birds. *Ecol. Monogr.* **56**, 327–344.
- Vermeij, G. J. 1991 When biotas meet: understanding biotic interchange. *Science* **253**, 1099–1104.
- Vermeij, G. J. 2004 Ecological avalanches and the two kinds of extinction. *Evol. Ecol. Res.* **6**, 315–337.
- Vitousek, P. M., D'Antonio, C. M., Loope, L. D., Rejmanek, M. & Westbrooks, R. 1997 Introduced species: a significant component of human-caused global change. *NZ J. Ecol.* **21**, 1–16.
- Warner, R. E. 1968 The role of introduced diseases in the extinction of the endemic Hawaiian avifauna. *Condor* **70**, 101–120.
- Winemiller, K. O. & Ponwith, B. J. 1998 Comparative ecology of eleotrid fishes in Central American streams. *Environ. Biol. Fishes* **53**, 373–384.
- Zaret, T. M. & Paine, R. T. 1973 Species introduction in a tropical lake. *Science* **182**, 449–455.

As this paper exceeds the maximum length normally permitted, the authors have agreed to contribute to production costs.

Visit [www.journals.royalsoc.ac.uk](http://www.journals.royalsoc.ac.uk) and navigate through to this article in *Proceedings: Biological Sciences* to see the accompanying electronic appendix.