

Life history traits and abundance can predict local colonisation and extinction rates of freshwater mussels

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SUMMARY

1. A critical need in conservation biology is to determine which species are most vulnerable to extinction. Freshwater mussels (Bivalvia: Unionacea) are one of the most imperilled faunal groups globally. Freshwater mussel larvae are ectoparasites on fish and depend on the movement of their hosts to maintain connectivity among local populations in a metapopulation.
2. I calculated local colonisation and extinction rates for 16 mussel species from 14 local populations in the Red River drainage of Oklahoma and Texas, U.S. I used general linear models and AIC comparisons to determine which mussel life history traits best predicted local colonisation and extinction rates.
3. Traits related to larval dispersal ability (host infection mode, whether a mussel species was a host generalist or specialist) were the best predictors of local colonisation.
4. Traits related to local population size (regional abundance, time spent brooding) were the best predictors of local extinction. The group of fish species used as hosts by mussels also predicted local extinction and was probably related to habitat fragmentation and host dispersal abilities.
5. Overall, local extinction rates exceeded local colonisation rates, indicating that local populations are becoming increasingly isolated and suffering an 'extinction debt'. This study demonstrates that analysis of species traits can be used to predict local colonisation and extinction patterns and provide insight into the long-term persistence of populations.

Keywords: colonisation, extinction, fish host, freshwater mussel, life history traits

Introduction

A critical need in conservation biology is to determine which species are most vulnerable to extinction. In general, abundant, widespread species have lower extinction rates than uncommon, narrowly distributed species (Angermeier, 1995). In particular, species with superior dispersal abilities are more likely to survive local extinction events than more range-restricted species (Bond, 1995). Most assessments of extinction risk have been based on the analyses of species–area relationships, isolation, and population sizes, essentially ignoring underlying ecological interactions (May, Lawton & Stork, 1995). However, links between species have important implications for extinction processes, and mutualistic and parasitic links between species may be especially critical (Dunn *et al.*, 2009; Kiers *et al.*, 2010; Spooner *et al.*, 2011).

Freshwater mussels (Bivalvia: Unionacea; hereafter 'mussels') are one of the most imperilled groups in the world (Strayer, 2008). In North America alone 72% of the native mussel fauna is either federally listed as endangered or threatened or considered to be in need of some protection (Haag, 2009). An understanding of the biological traits associated with the risk of extinction of mussels would greatly facilitate the conservation and management of this group. Mussels have unique life history traits that control their dispersal abilities and which can ultimately determine their distribution and abundance. The larvae (glochidia) of most mussels are obligate ectoparasites on the fins or gill filaments of fish. Adult mussels are sedentary, and dispersal to new habitat patches is dependent on host movement. However, mussels vary in the type and number of fish hosts used, the mechanism employed in infecting the host(s), and the timing of

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glochidial development and release (Barnhart, Haag & Roston, 2008). This variation has consequences for dispersal ability and population dynamics of mussels, and their distribution and abundance can be strongly influenced by the composition of the co-occurring fish assemblage (Watters, 1993; Haag & Warren, 1998; Vaughn & Taylor, 2000; Rashleigh, 2008; Schwab *et al.*, 2011a).

In streams, mussels often occur in multispecies aggregations called mussel beds. Mussel beds can range in area from <50 to >5000 m², and the density within such beds is typically 10–100 times higher than outside of beds (Vaughn & Spooner, 2006). While the habitat requirements of mussels are complex and not completely understood, mussel beds typically occur in river reaches that receive adequate flow during low water conditions but that also exhibit high substratum stability and low shear stress under flood conditions (Strayer, 2008; Allen & Vaughn, 2010). Mussel beds are often separated by stream reaches in which mussels are absent or rare; thus, the movement of mussels between mussel beds can only be accomplished through transport of glochidia attached to fish or perhaps via juvenile drift. Because of this, mussel beds function as local populations within an overall mussel metapopulation (Vaughn, 1993; Berg *et al.*, 1998; Skidmore *et al.*, 2010).

The purpose of this study was to determine which biological traits of mussel species best predict their risk of extinction. Metapopulation models describe a system of local populations or patches connected through dispersal and can be used to estimate species persistence in an area through comparison of local colonisation and extinction rates (Gotelli, 2001). I gathered data on the historical and present-day occurrence of 16 mussel species from the middle Red River drainage of Oklahoma and Texas. I then used these data to calculate local colonisation and extinction rates and to determine which mussel life history traits best predicted them.

Methods

Study area and sampling methods

Mussels are long-lived, iteroparous invertebrates with comparatively long generation times. Most species live longer than 10 years and some >100 years (Haag & Rypel, 2011). Age of first reproduction varies widely among species, ranging from <1 to >10 years (Haag & Staton, 2003). Thus, accurately estimating local colonisation and extinction rates for mussels requires historical presence/absence data that extend back many decades; such data are rare.

Isely (1924) conducted a comprehensive distributional survey of the mussel fauna of the middle Red River basin in Oklahoma and Texas, U.S.A., sampling 20 mussel beds on eight tributaries and one mainstem site in 1910–12. Six of Isely's (1924) original sites have subsequently been flooded by impoundments, leaving 14 intact sites spread throughout the drainage (Vaughn, 2000; Fig. 1). I assessed mussels at these 14 sites (Vaughn, 2000) during the summers of 1993–95 and used species presence–absence data to estimate local colonisation and extinction rates.

Mussels were sampled with semi-quantitative timed searches, which can be reliably used to locate rare species (Strayer & Smith, 2003). Timed searches were conducted by two experienced surveyors swimming systematically over the stream reach/mussel bed wearing a mask and snorkel and picking up mussels by hand. SCUBA was used in deeper areas (>75 cm). Mussels with siphons and/or shells exposed at the surface were located by both sight and feel; when a patch of mussels was located, surveyors also dug in the substratum in the search for buried mussels (Vaughn & Spooner, 2006). Total search time varied with mussel abundance, and more time was spent in larger mussel beds that contained more individuals; however, each site was searched for a minimum of 2 h. Mussels were identified and returned to the mussel bed alive after sampling was completed.

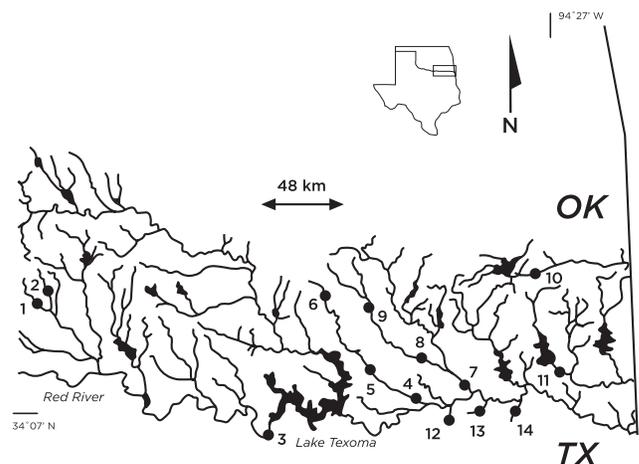


Fig. 1 Sites sampled in the Red River drainage of Oklahoma and Texas: West Cache Creek (1), Cache Creek (2), Red River (3), Lower Blue River (4), Blue River at Armstrong (5), Blue River north of Milburn (6), Lower Boggy Creek (7), Clear Boggy Creek at Boswell (8), Clear Boggy Creek at Olney (9), Kiamichi River at Tuskahoma (10), Little River at Garvin (11), Bois D'Arc Creek (12), Saunders Creek (13), Big Pine Creek (14). More detail is provided in Vaughn (2000).

Estimation of local colonisation and extinction rates

I used actual presence/absence data from the 14 sites to estimate local colonisation and extinction rates. Data were not adjusted by rarefaction (adjusting species richness for the number of individuals sampled) because there were differences in sampling methodology between the two surveys. Isely (1924) waded in shallow areas, whereas I used semi-quantitative timed searches that included deeper areas. Further, rarefaction is inappropriate when some species are clearly dominant (Bush, Markey & Marshall, 2004). Local (patch = mussel bed) colonisation (p_c) and extinction (p_e) rates were estimated for the 16 mussel species (Table 1) with a model that included both internal colonisation and the rescue effect, following Gotelli (2001). These rates range from 0 to 1 and represent the probability that a population at a particular site (mussel bed) will be colonised or lost. For each species, p_c is the number of sites colonised between the two time periods divided by the total number of sites unoccupied in the original survey. P_e is the number of sites that were occupied only historically divided by the total number of occupied sites (historical plus current occurrences). For each species, the number of available sites was defined as the sum of all the sites occupied by that species during at least one survey.

Mussel traits

Mussels were assigned to groups based on size, phylogeny, regional abundance and several life history traits (Table 1). Adult size groups based on mean shell lengths of species in the region (Vaughn & Taylor, 2000; Vaughn & Spooner, 2006) were as follows: small (<60 mm), medium (60–100 mm) and large (>100 mm). Tribe assignment was according to Graf & Cummings (2007). Regional abundance classes were based on the average density of each species for 30 sites across the region quantitatively sampled by Vaughn & Spooner (2006) and Vaughn & Taylor (2000). These were different sites than those sampled for presence/absence described earlier. The categories were as follows: highly abundant (more than 5 individuals m^{-2}), moderately abundant (1–5 individuals m^{-2}) and rare (<1 individual m^{-2}).

Assignment of mussels to primary groups of fish hosts and host generalists versus specialists was from the many sources in Table 1. In determining the fish hosts of mussel species, I excluded potential hosts for whom transformation has not been documented (e.g. see Watters & Cummings, 2010) and fish that were out of range in the study area (Miller & Robison, 2004). Mussels were assigned to primary host groups if those fish were most commonly named as hosts in the literature (i.e. occasional

Table 1 Traits of mussel species used in the analyses. Adult size groups are based on mean shell length of species from the region (Vaughn, 2000; Vaughn & Taylor, 2000). Tribes are according to Graf & Cummings (2007). Regional abundance is based on mean densities across the region (Vaughn & Taylor, 2000; Vaughn & Spooner, 2006). Assignment of the primary group of fish hosts, generalists versus specialists, primary host infection mode and brooding length is from multiple sources including Barnhart *et al.* (2008), Graf (1997), Graf & O'Foighil (2000), Haag (2009 and pers. comm.), Watters (2008), Watters *et al.* (2009), Watters & Cummings (2010), Williams *et al.* (2008) and Zanatta & Murphy (2006); fish hosts were only included if they were in range in the Red River drainage, and transformation on the host had been documented.

Species	Adult size (AS)	Tribe (TR)	Regional abundance (RA)	Primary host group (PH)	Generalist or Specialist (GS)	Primary host infection mode (MD)	Brooding length (BL)
<i>Amblema plicata</i> (Say)	Medium	Amblemini	High	Generalist	Generalist	No active host attraction	Short
<i>Fusconaia flava</i> (Rafinesque)	Small	Pleurobemini	Moderate	Minnows	Specialist	Active host attraction	Short
<i>Lampsilis cardium</i> (Rafinesque)	Medium	Lampsilini	Rare	Centrarchids	Specialist	Active host attraction	Long
<i>Lampsilis siliquoidea</i> (Barnes)	Small	Lampsilini	Rare	Generalist	Generalist	Active host attraction	Long
<i>Lampsilis teres</i> (Rafinesque)	Medium	Lampsilini	Rare	Gar	Specialist	Active host attraction	Long
<i>Lasmigona complanata</i> (Barnes)	Large	Anodontini	Rare	Generalist	Generalist	No active host attraction	Long
<i>Leptodea fragilis</i> (Rafinesque)	Medium	Lampsilini	Rare	Drum	Specialist	Unknown	Long
<i>Megaloniaias nervosa</i> (Rafinesque)	Large	Lampsilini	Rare	Generalist	Generalist	No active host attraction	Short
<i>Obliquaria reflexa</i> (Rafinesque)	Small	Lampsilini	Rare	Minnows	Specialist	Active host attraction	Short
<i>Potamilus purpuratus</i> (Lamarck)	Medium	Lampsilini	Rare	Drum	Specialist	Unknown	Long
<i>Ptychobranchnus occidentalis</i> (Conrad)	Small	Lampsilini	Moderate	Darters	Specialist	Active host attraction	Long
<i>Pyganodon grandis</i> (Say)	Large	Anodontini	Rare	Generalist	Generalist	No active host attraction	Long
<i>Quadrula pustulosa</i> (I. Lea)	Small	Quadrulini	Moderate	Catfishes	Specialist	Active host attraction	Short
<i>Quadrula quadrula</i> (Rafinesque)	Small	Quadrulini	Rare	Catfishes	Specialist	Active host attraction	Short
<i>Quadrula verrucosa</i> (Rafinesque)	Medium	Quadrulini	Rare	Catfishes	Specialist	Active host attraction	Short
<i>Truncilla truncata</i> (Rafinesque)	Small	Lampsilini	Rare	Drum	Specialist	Unknown	Long

instances were not used). Mussel species were categorised as specialists if they use only one fish species [e.g. drum, *Aplodinotus grunniens* (Rafinesque)] or a group of closely related species [e.g. darters (Percidae) and sunfishes (Centrarchidae)] as hosts (Haag & Warren, 2003). In contrast, I defined host generalists as mussels using a broad array of hosts across fish families.

Mussels have evolved different strategies for infecting fish with their parasitic larvae, ranging from broadcasting free larvae to elaborate mantle lures. Glochidia are generally bound by mucus into packets that either dissolve, releasing glochidia, or remain intact as discrete 'conglutinates' (Watters, 2008). Conglutinates can be loose structures that simply fall to the stream bed or elaborate structures that mimic the structure and colour patterns of a favoured prey item of the intended host, such as insect larvae and even larval fish (Barnhart *et al.*, 2008). When the fish bites into the conglutinate, glochidia are released and carried onto the gills by respiratory currents. Mantle lures, found in the Lampsilini, are pigmented modifications of the mantle that mimic prey items (i.e. minnows, crayfish) of predacious fish. These flaps surround the swollen gills (marsupia) where the female broods the glochidia. Gravid females extend their posterior shell margins above the substratum and periodically move the mantle flaps to resemble swimming prey fish. When a host fish attacks the mantle flaps, the gills are ruptured and glochidia are released and carried onto the gills by respiratory currents (Barnhart *et al.*, 2008). Mantle magazines, found in the Quadrulini, function similarly to lures. For this analysis, I defined *no active host attraction* (NA) to include mussel species that broadcast free larvae [e.g. *Megaloniaias nervosa* (Rafinesque)], those that release larvae into a mucus web [e.g. *Pyganodon grandis* (Say)] and those that deposit loose conglutinates without specialised adaptations to attract host fish [e.g. *Amblema plicata* (Say)]. I defined *active host attraction* (A) as species that attract hosts via conglutinates, mantle lures or mantle magazines. Many mussel species employ more than one glochidial release mechanism. For example, species with mantle lures typically also release fragile conglutinates late in the breeding season to make room for new brood (Barnhart *et al.*, 2008). For this analysis, I assigned mussels to categories based on what is indicated by the literature to be their primary infection mode or strategy.

I used Graf & O'Foighil's (2000) interpretation of short-term and long-term broodings. Short-term brooders retain glochidia in the gills only until they reach maturity; glochidia are not brooded after they become infectious. While most short-term brooders produce gametes in the spring and release glochidia in the late spring or summer,

the cycle can also take place in the autumn and winter. Long-term brooders continue to brood their glochidia after they become infectious. They typically spawn in late summer, brood glochidia over the winter and release them in the late spring.

Data analysis

I used general linear models (SPSS; IBM, Armonk, NY, USA) to examine which mussel traits could best predict local colonisation and extinction rates. As suggested by Burnham & Anderson (2002), starting model parameters were selected *a priori* based on patterns that demonstrated differentiation between trait groups in Fig. 2. I used Akaike's information criterion (AIC) to select the best models by comparing each of the candidate models simultaneously. I converted AIC to small-sample AIC_c and calculated Akaike weights (w_i). The best performing models are those with the lowest AIC_c and the highest w_i (Burnham & Anderson, 2002). For each dependent variable, I also compared the models with a null (intercept only) model. Only the top six models are shown for each dependent variable.

Results

Averaged across species, local extinction rates significantly exceeded local colonisation rates throughout the region (Fig. 3). On the basis of the average Akaike weights (w_i) from AIC_c selection, models combining host infection mode and whether a mussel was a generalist or specialist best predicted local colonisation rates (Table 2). Host infection mode was particularly important; models containing host infection mode (MD) had a summed w_i of 0.912. The average R^2 for models with $\Delta_i < 2$ (MD + GS, MD; see Table 1 for abbreviations) was 0.30, and generalists versus specialists (GS) contributed an additional 21% to the amount of variation explained by host infection mode alone. The Δ_i of the null model was 13.465, much greater than any of the six top models.

Models incorporating brooding length, primary groups of fish hosts, tribe and regional abundance best predicted local extinction rates (Table 2). Models containing brooding length (BL) had a summed w_i of 0.566, and models containing primary host group (PH) had a summed w_i of 0.748. The average R^2 for models with $\Delta_i < 2$ (all models shown: BL, PH, BL + PH + TR + RA, BL + PH + TR, PH + TR, PH + TR + RA) was 0.28. While brooding length and primary host group were the top models, adding regional abundance (RA) and tribe (TR) to these models increased the amount of variance explained by over 10%.

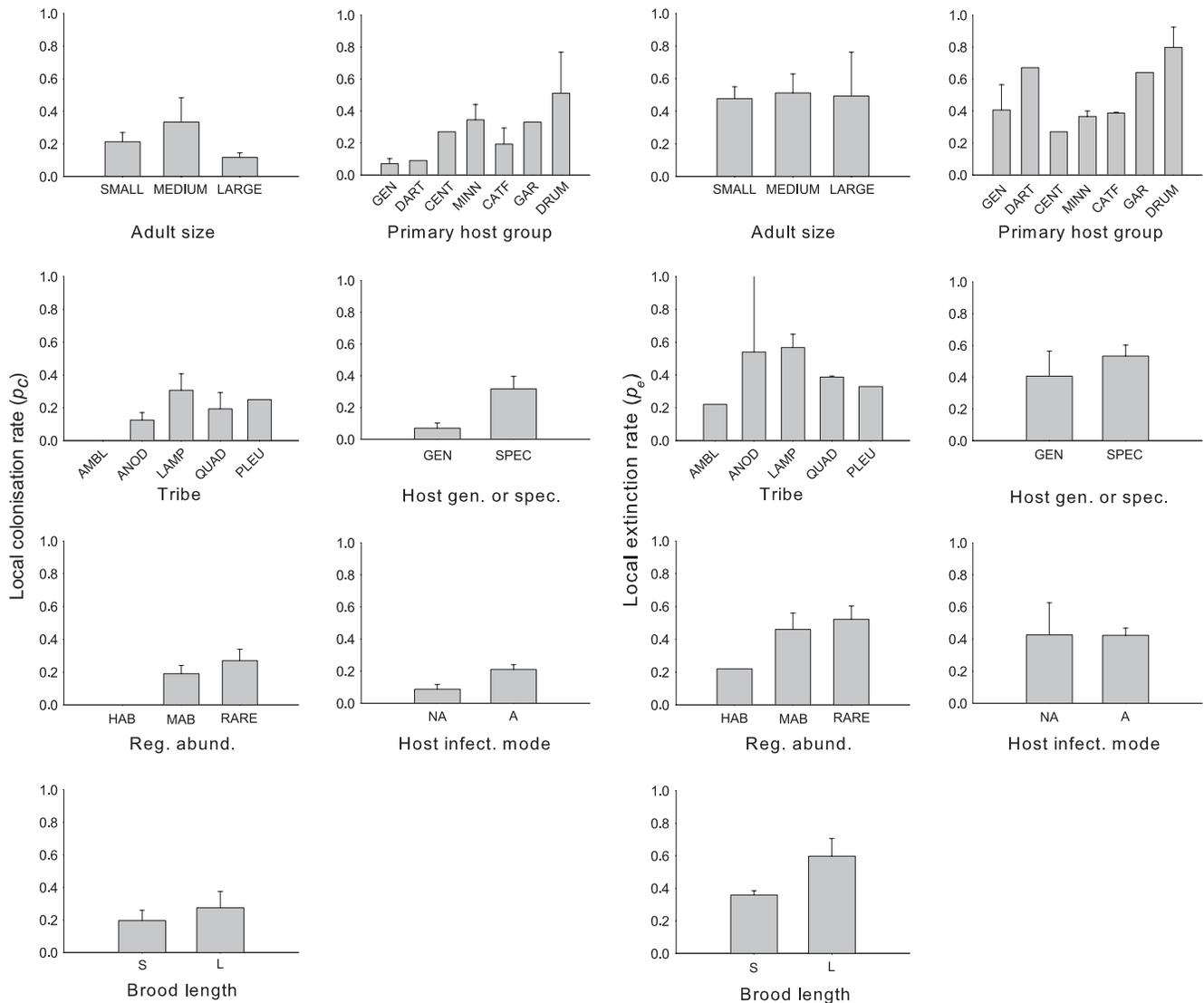


Fig. 2 Mean (± 1 SE) local extinction and colonisation rates by mussel trait groups from Table 1.

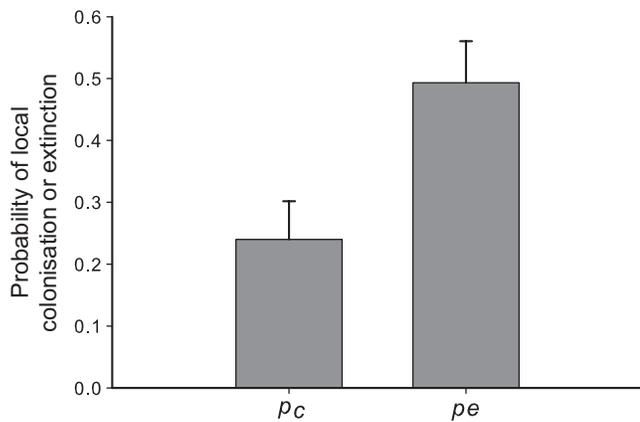


Fig. 3 Mean (± 1 SE) local colonisation and extinction rates for the 14 sites ($t = -2.771$, $P = 0.01$).

Local extinction models were not as strong as local colonisation models. The Δ_i of the null model was 2.043, only slightly greater than the weakest explanatory model.

Discussion

Long-term persistence of metapopulations depends on the migration of new individuals with different genetic material between local populations. For mussels, this migration must occur mainly via movement of fish hosts, and successful colonisation of a new patch should be a function of both the ability to infect the host and the host's distribution, abundance and movement patterns. My data support this premise; local colonisation rates were best predicted by host infection mode and whether a mussel

Table 2 Summary of small-sample Akaike information criterion (AIC_c) selection of models predicting local extinction and colonisation rates

Rank	Model	R ²	K	Δ _i	w _i
Local colonisation					
1	MD + GS	0.40	4	0.000	0.525
2	MD	0.19	3	1.031	0.314
3	GS + RA	0.48	4	3.608	0.086
4	MD + RA	0.23	4	4.978	0.043
5	MD + GS + RA + BL	0.48	6	6.720	0.018
6	MD + RA + BL	0.27	5	7.505	0.012
Local extinction					
1	BL	0.21	3	0.000	0.251
2	PH	0.18	3	0.876	0.162
3	BL + PH + TR + RA	0.36	6	0.885	0.161
4	BL + PH + TR	0.32	5	0.978	0.154
5	PH + TR	0.31	4	1.184	0.139
6	PH + TR + RA	0.35	5	1.287	0.132

K = number of parameters in the model + 2, Δ_i = AIC_c of model relative to lowest AIC_c, w_i = Akaike weight. Only the six best performing models are shown, and all of these performed better than a null model (local colonisation null model Δ_i = 13.465, local extinction null model Δ_i = 2.043). Abbreviations for variables are given in Table 1.

was a host generalist or specialist. Mussel species that used host-attracting strategies, such as conglutinates and lures that resembled prey items, had higher local colonisation rates, and mussels that specialised on one or a small group of host fish also had higher local colonisation rates (Fig. 2). These two traits often co-occur; most mussel species are host specialists (Haag & Warren, 2003) and species that use host-attracting strategies often specialise on a small number of closely related hosts that respond to that strategy, such as bass and sunfish, minnows and darters (Barnhart *et al.*, 2008). Combined, these traits are believed to decrease the competition for fish hosts by allowing mussels to 'lure' hosts in a density-independent fashion (Haag & Warren, 1998; Barnhart *et al.*, 2008). In addition, although host-attracting mussels may rely only on a few species of hosts, these hosts are often abundant and widespread (Watters, 1993). Thus, both of these life history traits (actively attracting a host and being a specialist) should increase the probability of a propagule dispersing to a new patch, which is what these data demonstrate.

In contrast to local colonisation, local extinction rates should depend on whether local populations are of a viable size (Gotelli, 2001). In this study, local extinction rates were best predicted by a combination of brooding length, tribe, regional abundance and primary host group. The first three factors are all related to mussel abundance and thus local population size. Highly abundant species

had the lowest local extinction rates and rare species the highest. In addition, short-term brooders had lower extinction rates than long-term brooders. Short-term brooders, particularly *A. plicata*, were the most abundant species in the region (Table 1). Short-term brooders may be replacing themselves more frequently than long-term brooders, which would contribute to their higher regional abundance. Some short-term brooders can produce multiple broods per year, particularly at warmer latitudes (Parker, Hackney & Vidrine, 1984; Heard, 1998; Price & Eads, 2011). I have observed gravid *A. plicata* throughout the year in southern Oklahoma and think it is likely that this species and other short-term brooders are producing multiple annual broods in this region. Alternatively, lower extinction rates of short-term brooders may be due to other, unmeasured factors that are correlated with brooding period. The most abundant short-term brooders in this study, *A. plicata* and *Fusconaia flava*, are physiologically more tolerant of the warm summer temperatures prevalent in this region (Spooner & Vaughn, 2008). In a 20-year study of one river in the region (Kiamichi River), Galbraith, Spooner & Vaughn (2010) found that these thermally tolerant species increased in abundance relative to more thermally sensitive species in pools isolated by drought. If thermally tolerant species that also happen to be short-term brooders are better able to survive and reproduce in fragmented rivers stretches, this would lead to a lower extinction rate, as observed. Local extinction rates were also related to tribe, which probably reflects both species brooding behaviour and physiology, as the abundant short-term brooders, *A. plicata* and *F. flava*, are both thermally tolerant and were the single representatives of the tribes Amblemini and Pleurobemini. Unfortunately, I did not have thermal tolerance data for most of the species examined here and thus could not use it as a trait in the analysis.

Local extinction rates could also be predicted by primary fish host group. Mussel species with the highest extinction rates used gar, drum and darters as hosts. Like most rivers globally, the streams in this study have become fragmented by impoundments resulting in increasingly isolated local mussel populations (Vaughn & Taylor, 1999; Vaughn, 2000; Galbraith *et al.*, 2010). Factors leading to the decline of isolated mussel populations may also affect isolated fish host populations (Quinn & Kwak, 2003; Gido, Dodds & Eberle, 2010), which could lead to a decrease in the abundance of host fish and fewer host choices for mussels (Layzer & Scott, 2006; Berg *et al.*, 2008; Spooner *et al.*, 2011). High local extinction rates of mussel species using gar, drum and darters probably reflect decreased access to these fish hosts, either through

absolute decline in fish host abundance or because these hosts cannot overcome barriers such as dams.

Gar and drum typically swim long distances (Minns, 1995; Snedden, Kelso & Rutherford, 1999; Albanese, Angermeier & Peterson, 2009). Fragmentation blocks the movement of fish hosts or increases the distance they must travel, particularly for fish with large home ranges (Woolnough, Downing & Newton, 2009), and several studies have documented lower densities of riverine fishes in areas upstream of dams (Neves & Angermeier, 1990; Winston, Taylor & Pigg, 1991; Quinn & Kwak, 2003; Gido *et al.*, 2010). Watters (1996) found that the decline of two mussel species above low head dams was directly linked to the inability of their host, freshwater drum, to move above the dams, and other studies have linked the decline or restricted movement of fish by dams to the decline of upstream mussel populations (Smith, 1985; Kelner & Sietman, 2000; Brainwood, Burgin & Byrne, 2008). Even without habitat fragmentation, however, mussels that use host fishes that swim long distances might have a higher probability of being deposited in unfavourable habitat.

In contrast to gar and drum, darters typically have very low dispersal rates, often moving more than 100 m in their lifetime (Freeman, 1995; Petty & Grossman, 2004; McClain & Ross, 2005). In a study of the endangered snuffbox mussel (*Epioblasma triquetra* Rafinesque), Schwalb, Poos & Ackerman (2011b) found 82% of recaptures of the host, the logperch [*Percina caprodes* (Rafinesque)], were within 30 m of their original point of capture. Albanese *et al.* (2009) found that fish species with low mobility recover more slowly following local extinctions. Darters occupy smaller streams than the large, migratory gar and drum discussed previously. In this study, high local extinction rates associated with darters probably reflect increasing isolation of fish host populations, as small tributaries become isolated from one another by the construction of dams on the larger river connecting them (Haag, 2009).

Adult size did not predict local colonisation or extinction. Fecundity increases with adult size in many species with indeterminate growth. I thus expected adult size to decrease extinction rates and increase colonisation rates, because of positive correlations between size and lifetime fecundity (Downing *et al.*, 1993; Haag & Staton, 2003). I did not find this relationship, either because it is only important within (not among) species, owing to sample size constraints, or because reproductive strategies such as luring of host fish are independent of adult size.

The small sample sizes of sites, species and species traits limit generalisations from this study. While all the

models had lower Δ_i than the null models, overall R^2 values were low, indicating that factors additional to the ones used in the model comparison also influence colonisation and extinction rates. Mussel species vary in multiple traits in addition to the reproductive and thermal traits discussed earlier (Vaughn, 2010). Lifespan, fecundity and age at first and last reproduction should be particularly important for predicting local colonisation and extinction rates because they influence the number of reproductive events and propagule success (Bauer, 1992, 1998). In this study, models predicting local extinction were weaker than models predicting local colonisation, when compared to a null model. As discussed above, local extinction rates should be related to population size. In turn, population size should be directly related to the number of reproductive events. Thus, inclusion of these important life history traits would probably have strengthened the extinction models. Future studies should incorporate these life history traits, all which can be relatively easily measured (Haag & Staton, 2003; Moles & Layzer, 2008; Galbraith & Vaughn, 2011), other species traits, and be performed across a larger spectrum of mussel species and sites.

Caution should be used when inferring temporal changes in mussel populations based on presence-absence data from a limited number of sites (Strayer, 1999). Isely's (1924) field techniques were fairly quantitative for the time; for example, he discusses the use and value of replicate samples and the problems using mark/recapture techniques (Isely, 1931). However, Isely (1924) sampled by wading and picking up mussels, and I sampled by systematically snorkelling sites and by digging into the substratum. Because my sampling method was more rigorous than that of Isely (1924), any sampling error should be in the direction of finding more species in the contemporary than the historical survey. That is, there is a high probability that I might find a species that he missed, and thus overestimate colonisation rates, but a low probability that I would miss a species that he found, and thus underestimate extinction rates. Therefore, the conclusion that local extinction rates exceeded local colonisation rates in the region is probably sound.

The formula for p_e can underestimate extinction rates if multiple extinctions and re-colonisations occur over the sampling period (Angermeier, 1995; Gotelli, 2001). This scenario is unlikely here as mussels are extremely long-lived. Most species live longer than 10 years and some more than 100 years (Haag & Rypel, 2011). Reproductive maturity is generally delayed, and some species may not reproduce every year (McMahon & Bogan, 2001; Haag &

Staton, 2003). Thus, the 80-year gap between Isely's (1924) collections and the contemporary survey is likely to represent only a few generations of most species. In addition, colonisation rates for all species in the system were quite low, with most sites only experiencing extinctions during the 80-year time period (Vaughn, 2000).

Over a decade ago, Ricciardi & Rasmussen (1999) predicted a future extinction rate of freshwater mussels at 6.4% per decade, and numerous studies have documented abundance declines of once widespread, common mussel species (e.g. Neves *et al.*, 1997; Vaughn & Taylor, 1999; Anthony & Downing, 2001; Brainwood, Burgin & Byrne, 2006; Krebs *et al.*, 2010). The relative immobility, long lifespan and reproductive characteristics of freshwater mussels make them particularly vulnerable to habitat disturbance, especially habitat fragmentation (Strayer, 2008). In this study, mean local extinction rates were significantly greater than mean local colonisation rates, indicating that local populations are becoming increasingly isolated. In such isolated populations, declines in population size from either anthropogenic or natural causes cannot be compensated for by infrequent migration from other local populations, resulting in a downward spiral of abundance (Berg *et al.*, 2008; Haag, 2009). In metapopulation terminology, habitat fragmentation leaves these local populations more prone to extinction because they are isolated from 'rescue' by immigration (Gotelli, 2001). As local populations decline or are eliminated and dispersal distances are increased, demographic and genetic constraints will diminish the ability even of currently abundant species to respond to natural disturbance and much less to anthropogenic change (Vaughn, 1993). Genetic constraints have already been documented in the middle Red River drainage. Reagan (2008) found that fragmentation by impoundments significantly decreased genetic variability in populations of *A. plicata* in southern Oklahoma.

Recently, both Haag (2009) and Strayer (2008) discussed the extinction debt (future extinction of species owing to past events; Tilman *et al.*, 1994) associated with habitat fragmentation. Because mussels are long-lived, there is a time lag between populations becoming isolated and finally going extinct. During the peak of dam construction in the 1920s–70s, many populations of obligate large river mussel species were lost owing to direct habitat destruction. However, most tributary mussel species survived in local populations now isolated from one another by the loss of connecting large river habitat, leaving an extinction debt. We are now seeing this extinction debt repaid as isolated tributary populations go locally extinct (Haag,

2009), and the data from the Red River drainage support this pattern.

Species vary in their vulnerability to extinction. As Angermeier (1995) has pointed out, species extinctions are rarely because of single catastrophic events. Rather, species extinctions are preceded by the loss of local populations. As this study demonstrates, analysis of local colonisation and extinction patterns can provide insight into the long-term persistence of populations. The challenge to conservation biologists is to identify the important factors leading to local extinctions, and an examination of species traits is an important step in this process.

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