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## Habitat Constraints and the Generation of Diversity in Freshwater Macroinvertebrates

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### Abstract

Freshwater aquatic invertebrates occupy a range of habitats, which can broadly be classified into running or standing waters. The contrasting habitat permanence over geological timescales of these two habitat types imposes different constraints on their invertebrate populations. Species in more ephemeral lentic water bodies are forced to disperse when the habitat disappears, and are thus predicted to have higher dispersal abilities and inter-population gene flow, resulting in larger, more dynamic geographical ranges and slower evolutionary turnover. In the more stable lotic habitats, species are predicted to have lower dispersal abilities, with higher persistence of local populations and reduced inter-population gene flow. This should result in smaller range sizes and a higher evolutionary turnover. Latitudinal diversity gradients of lentic and lotic species may also be expected to differ, as lotic species will be more dependent on historical factors and distance to glacial refugia, whereas lentic species will be closer to an equilibrium with current ecological and geographical conditions. Some of these predicted patterns have been demonstrated for a range of aquatic invertebrates across different geographical areas, although the underlying evolutionary and physiological mechanisms are still poorly understood.

### Introduction

Spatial gradients in species richness are among the best documented and most robust ecological patterns (reviews in Brown, 1995; Gaston and Blackburn, 2003). Most of these patterns, however, remain descriptive, and there are still few answers to basic questions such as why closely related species may have widely different geographical ranges (Lester *et al.*, 2007). Despite the multiple explanations put forward, such as differences in niche breadth, body size, population abundance, environmental variability, colonization and extinction dynamics, and dispersal ability (Stevens, 1989; Brown, 1995; Gaston, 2003; Lester *et al.*, 2007), there are few data to allow any general conceptual framework beyond the counts of species numbers and their statistical correlates. The Habitat Templet

concept (Southwood, 1977, 1988; Korfiatis and Stamou, 1999) may provide the basis for such a framework. In Southwood's concept, the habitat is the templet that drives the evolution of organisms, such that the constraints posed by the habitat characteristics influence the ecological traits of the species living on it. In freshwaters, one of the most influential of these habitat constraints is the divide between standing (lentic) and running (lotic) waters (see Harrison and Dobson, Chapter 13, this volume, for the effect of other types of ecological and biological constraints). This should not be interpreted in terms of intensity of water flux only, but in a wide range of associated physical and biological characteristics. Despite the existence of unavoidable grey areas, most of the freshwater habitats in which macroinvertebrates are commonly found (and studied) can be generally assigned to one of these two types. In a series of papers, Ribera and Vogler (2000) and Ribera *et al.* (2001, 2003) explored the possible implications of the different constraints that these two habitat types could impose on the populations, species and lineages living in them.

In the following chapter, I will first summarize the hypothetical model of how habitat type may influence the macroecology and macroevolution of species and populations of freshwater invertebrates. The assumptions of this model will be supported using data from other organisms and ecosystems (i.e. not necessarily related to freshwater habitats, or particularly to the lotic/lentic divide). Second, I will detail the results of the research with the explicit aim of testing the implications of the lotic/lentic habitat preferences. The review will end with a comment on possible caveats, problems to be solved and suggestions for further research.

## **An Integrated Framework for some Macroecological and Macroevolutionary Patterns in Freshwater Macroinvertebrates**

Small- to medium-sized standing water bodies, such as those typically inhabited by many groups of aquatic macroinvertebrates, are generally short-lived and discontinuous in time and space (Hutchinson, 1957). Once a particular water body disappears, there is no direct physical connection to any other similar habitat. In contrast, running water bodies generally persist over longer geological periods and remain connected to other water bodies within the drainage network, despite changes in the exact location of the channel. The temporal scale of these differences is much longer than the possible seasonal variations within the lifespan of individual habitats; streams in some areas (e.g. Mediterranean) may be seasonal and dry regularly, but their long-term persistence is unaffected. Most freshwater macroinvertebrate species can be categorized as inhabiting either lentic or lotic waters, with comparatively few species able to inhabit both (Illies, 1978; Foster *et al.*, 1992; Larson, 1997; Ribera and Vogler, 2000). Differences in habitat preference occur at all phylogenetic levels, often among sister species, or groups of closely related species (Ribera *et al.*, 2001). Many insect groups have colonized freshwaters several times independently and, hence, provide independent replicates of the influence of habitat on insect ecology.

The contrasting habitat permanence of lotic and lentic waters is predicted to lead to a cascade of ecological and evolutionary implications ranging from the

individual to the lineage (Table 15.1). Critically, species living in geologically long-lived habitats will be expected to have reduced dispersal ability compared with those species living in geologically more ephemeral habitats. It must be stressed that the term 'dispersal' is taken to mean the ability of a species to establish a new population in a non-contiguous habitat patch (i.e. emigration plus inter-patch movement plus immigration, *sensu* Bowler and Benton, 2005), but not 'dispersal' as movement of individuals, *sensu* Bilton *et al.* (2001). In the sense used here, dispersal may, or may not, be correlated with the ability of individuals to migrate or to travel long distances.

The higher mobility and colonization ability of populations of lentic species will then lead to more dynamic and larger geographical ranges, faster colonization of new areas (e.g. after deglaciation or of islands), lower beta diversity and a greater occupancy of potential niches than lotic species. Lotic species are predicted to be more sensitive to global change, as they will have more difficulty tracking rapid changes in a discontinuous habitat matrix. The higher mobility of lentic species is also predicted to increase gene flow between populations, resulting in reduced inter-population genetic variability and thus leading to a greater evolutionary cohesion of species. Over comparable geographical scales, this is predicted to lead to a less pronounced phylogeographical structure and a decreased probability of peripatric or allopatric speciation for lentic species. Their larger geographical range will further reduce the probability of extinction.

When habitat preferences or the size of the geographic range are maintained across speciation events, or the physical setting of an area favours the dominance

**Table 15.1.** Summary of the predicted characteristics of the populations, species and lineages living in lotic or lentic habitats, according to the model outlined in the text.

Populations/species	Lotic	Lentic
<i>Geographic range</i>		
Overall size	–	+
Edge dynamics (range shifts)	–	+
Frequency of 'outliers'	+	–
Colonization of new areas (deglaciated, islands)	–	+
Latitudinal gradients	+	–
Geographical turnover (beta diversity)	+	–
Fit between realized and potential distribution	–	+
Sensitivity to global change	+	–
<i>Genetic flow</i>		
Evolutionary cohesion of the species	–	+
Filogeographical structure	+	–
Probability of peripatric or allopatric speciation	+	–
Probability of extinction	+	–
Intrapopulation genetic variability	–	+
Age (intraspecific coalescence)	–	+
<i>Lineages</i>		
Evolutionary turnover	+	–
Propensity to generate radiations	+	–

of running or standing habitats for long periods of time (enough for successive cladogenetic events in the same lineage), it is expected that the consequences of habitat constraints will extend to macroevolutionary characteristics of whole lineages (Gould, 2002). The lower probability of speciation and extinction in lentic species would result in a lower evolutionary turnover, which would be higher in lotic species. On average, lentic species are thus expected to be older, with larger intraspecific genetic variability. Note that the higher probability of extinction in lotic clades increases the likelihood that the 'true' sister of a species is extinct, i.e. that the extant closest relative (the observed sister) may actually be rather distant. Ages of the species would thus have to be measured using the coalescent time and not the distance to their extant sisters.

The higher persistence of local populations, together with smaller geographical ranges and reduced gene flow, favours the specialization of lotic species. If this was the case, it seems likely that this could bias the probability of habitat shifts as, once a lotic specialization is established, the possibility of a transition to a lentic habitat may be impaired.

The total number of species within a clade at any given time will depend on the balance between speciation and extinction. As the same general factors promoting speciation also favour extinction (Stanley, 1979; Hubbell, 2001; Gould, 2002; Jablonski, 2007), there are no clear predictions as to which habitat type would promote higher species diversity at any given time (i.e. synchronic diversity), as opposed to the expected higher accumulated diversity of lotic lineages through time (i.e. diachronic diversity). However, the predicted high turnover in lotic species means that the potential for both fast radiations and complete extinction of whole lineages may be higher than in lentic species.

## Justification of the Assumptions

Most of the assumptions of the model outlined above have been documented for different groups of organisms in different systems, but only rarely with aquatic insects.

## Relationship between dispersal ability and geographical range

Despite much attention, the relationship between dispersal ability and size of the geographic range remains contentious (e.g. Lester *et al.*, 2007). As noted above, we need to distinguish between 'movement' and 'establishment' of individuals/populations. Standard measures of 'dispersal ability' are often only surrogates of the distance that individuals can travel, not of the ability of reaching a distant suitable habitat patch and establishing a new population. In some cases it may be assumed that there is no restriction to movement, and differences in dispersal ability relate only to the ability to establish new populations (e.g. plants in the arctic, Alsos *et al.*, 2007; some planktonic organisms, De Meester *et al.*, 2002). It is unsurprising, therefore, that the evidence for a strong relationship between dispersal ability and range size is equivocal (e.g. marine organisms, Lester *et al.*,

2007; moths, Beck and Kitching, 2007), although there are many examples of a positive correlation (presence of wings in beetles, Juliano, 1983; wing size in damselflies, Rundle *et al.*, 2007; flying ability in warblers, Böhning-Gaese *et al.*, 2006). In plants, dispersal ability is often measured in relation to mode of pollination or seed size, and a positive relationship between these surrogate measures and size of the geographical range has been reported (e.g. in New Zealand, Lloyd *et al.*, 2003; trees, Morin and Chuine, 2006; but see Lowry and Lester, 2006 for an opposite trend).

For marine organisms, it is generally accepted that species with feeding pelagic larval forms have larger ranges than species with direct, non-pelagic development or non-feeding larvae (gastropods, Scheltema, 1989; sea urchins, Emllet, 1995; Jeffery and Emllet, 2003; teleost fishes, Goodwin *et al.*, 2005; Indo-Pacific fishes, Lester and Ruttenberg, 2005). However, the relationship between range size and the duration of the planktonic larval stage is either equivocal, or non-existent (Scheltema, 1989; Lester *et al.*, 2007; Victor and Wellington, 2000).

When looking at surrogates of dispersal ability, it is also important to account for ecological or biological characteristics of the different groups. For example, while oviparous species of teleost fishes have larger ranges than viviparous species (Goodwin *et al.*, 2005), the opposite is true for elasmobranchs, where eggs of oviparous species are fixed and develop in situ, so that the egg is not a dispersal stage, as in teleosts.

### **Relationship between dispersal ability and gene flow/phylogeographic structure**

The relationship between range size and phylogeographic structure has received much less attention than that between range and dispersal ability, probably because of the difficulty in obtaining suitable data. Several recent studies, however, support the prediction that, at similar geographical scales, species of lower dispersal ability have a more pronounced phylogeographic structure. In two closely related species of water mite, the one (*Arrenurus angustilimbatus*) with larvae that ecto-parasitize and disperse on adult mosquitoes possesses a broader and more continuous geographic distribution, with higher allozyme heterozygosity and less population differentiation, than the species (*A. rufopyriformis*) with larvae that do not ecto-parasitize mosquitoes and have more limited dispersal abilities (Bohonak *et al.*, 2004). Comparing two more distantly related species (Ephemeroptera and Amphipoda) with contrasting dispersal abilities, Zickovich and Bohonak (2007) report similar differences in genetic structure.

In marine organisms, the mode of development is a determining factor of phylogeographic structure. Species with direct development (embryonic development taking place through yolk feeding in an egg capsule or egg mass deposited directly on the substrate with no pelagic stage) have higher levels of population structure than do species with planktonic development (e.g. gastropods, Collin, 2001; corals, Hellberg, 1996; sea cucumbers, Arndt and Smith, 1998; fishes, Hunt, 1993; Riginos and Victor, 2001). Within marine cowries, species that possess planktonic larvae have greater mean pairwise genetic distance within each taxon

than species without planktonic larvae (and hence having restricted dispersal and narrow ranges) (Meyer and Paulay, 2005). In this study, intraspecific variation (as measured by depth of coalescence) was uncorrelated with interspecific divergence, indicating that 'older' species (those without close extant relatives) do not have more intraspecific variation than 'younger' species (those with close living relatives).

In a review of factors determining genetic structure in plants, Duminal *et al.* (2007) found few significant traits, but among them were seed dispersal mode and geographic range size. For example, wind pollinated species of palms had lower population genetic structure, as measured with allozymes, than coexisting species with entomophilous pollination and lower seed dispersal abilities (Luna *et al.*, 2005).

### **Relationship between range size and probability of speciation/extinction**

There is considerable evidence of species with larger ranges having a lower probability of extinction, but the relationship with probability of speciation is less clear. Most of this evidence is from the fossil record of marine invertebrates. The classic work of Hansen (1980) demonstrated that in lower Tertiary gastropods in the Gulf coast of North America, widespread species with planktonic larvae survived longer, a result that has been confirmed subsequently by different works (e.g. Jablonski, 1987; Gili and Martinell, 1994; Jeffery and Emler, 2003; Foote *et al.*, 2007). Species without planktonic larvae could attain wide geographic ranges when barriers to dispersal were minimized, but could not maintain these wide distributions during periods of habitat fragmentation caused by delta formation within the Gulf, when the isolation of populations accelerated extinction (Hansen, 1980). Payne and Finnegan (2007) found that the geographic ranges of genera of fossil, benthic marine invertebrates were positively correlated with survival in 'normal' background extinction periods, irrespective of species richness and abundance, although not in periods of mass extinctions. Liow (2007) also reported a positive relationship between latitudinal and bathymetric range extension, and species longevity for marine Ostracoda. Based on extant species, higher probabilities of extinction have been linked with reduced geographical range in freshwater fishes (Rosenfield, 2002), primates and carnivores (Purvis *et al.*, 2000).

The relationship between geographical range size and speciation rate has been addressed more rarely. Gavrillets *et al.* (2000) used simulations to show that species with smaller range sizes (characterized by smaller local densities and reduced dispersal ability) should have higher speciation rates. Jablonski and Roy (2003) provided data for Late Cretaceous gastropod genera, which exhibit a strong negative relationship between the geographical ranges of constituent species and speciation rate per species per million years, showing that the factors promoting broad geographical ranges also tend to dampen speciation rates. Using data of extant species of Australian arid and semi-arid plants, Akwood *et al.* (1993) found that species adapted for long-range dispersal may have experienced lower speciation rates. Lester and Ruttenberg (2005) revealed a negative correlation between species richness and larval duration at the family level in Indo-Pacific

tropical reef fishes, implying that speciation rate may be negatively related to dispersal potential. A negative relationship between speciation rate and range size is not always found, however (Rosenzweig, 1995). Cardillo *et al.* (2003) reported faster diversification rates for species with larger geographical ranges and larger litters among Australian mammals, although they attribute this difference to a decreased probability of extinction and not to an increased speciation rate.

### **Inheritability of habitat preferences ('niche conservatism')**

The retention of ecological characteristics within species lineages ('niche conservatism') is well established (e.g. reviews in Wiens, 2004; Wiens and Graham, 2005), particularly for broad traits such as general habitat preferences. Although habitat shifts must occur, even among sister species (e.g. aquatic Coleoptera, Ribera and Vogler, 2000; Ribera *et al.*, 2003), species lineages, in general, tend to have a preferred or exclusive habitat type, allowing us to investigate the long-term macroevolutionary consequences of habitat constraints (e.g. Ribera *et al.*, 2001).

### **Inheritability of species-level traits (size of the geographic range, speciation rates)**

The classic work of Jablonski (1987) has been until recently virtually the only published evidence of the possible inheritability of a species-level character such as the size of the geographic range. This finding has been contested by Webb and Gaston (2003, 2005) who, after re-analysing the same data set, found little support for the notion that species selection on geographic range sizes has played a significant role in shaping contemporary species–range size distributions, in disagreement with Hunt *et al.* (2005) and Jablonski and Hunt (2006). However, Mouillot and Gaston (2007), in a reappraisal of the question using a modelling approach, accept the possibility of significant heritability in the geographical range sizes of species, even without any biological trait differences. The heritability found was weaker than that observed in empirical studies, but suggests that a substantial component of heritability may not necessarily be associated with niche conservatism at the individual level. Waldron (2007) reviews the question of the heritability of geographical ranges, using a range of models and Nearctic birds as examples. In addition to reaffirming the non-randomness of the distribution of the size of geographical range in a phylogeny, the most relevant result is that current ranges of sister species are more symmetrical than expected at the moment of speciation. This means that biological or ecological characteristics of the species (kept through the cladogenetic event) constrained the subsequent evolution of the geographical range after speciation, increasing the observed similarity between sisters.

The evidence supporting sustained differences in speciation rates, due to inheritance of species traits, is even more scarce and generally inconclusive (e.g. Duda and Palumbi, 1999; Jeffery and Emler, 2003). Savolainen *et al.* (2002) explicitly addressed the inheritability of cladogenesis characteristics. By looking at the size of the branches in linearized trees, they found a pattern for most of the

studied clades consistent with heritable net cladogenesis. These authors claim that heritability of cladogenesis may be a general phenomenon, detectable across a large number of lineages and a broad range of taxa. Gould (2002) also discusses extensively the macroevolutionary implications of sustained biases in cladogenetic processes, supporting the view that continuous habitat constraints (as would be landscape characteristics favouring the presence of either lotic or lentic habitats) could be determining factors in the macroevolutionary characteristics of whole lineages. In any case, the very existence of species radiations (i.e. lineages significantly more diverse than their sisters) may be taken as a proof of the maintenance in some lineages of 'higher than average' diversification rates across several cladogenetic events.

## Testing the Predictions in Freshwater Ecosystems

This section reviews the work specifically addressing the macroecological or macroevolutionary implications of the lotic and lentic habitat constraints in freshwater invertebrates. The chain of inferences derived from the basic assumptions described above is used as a guide.

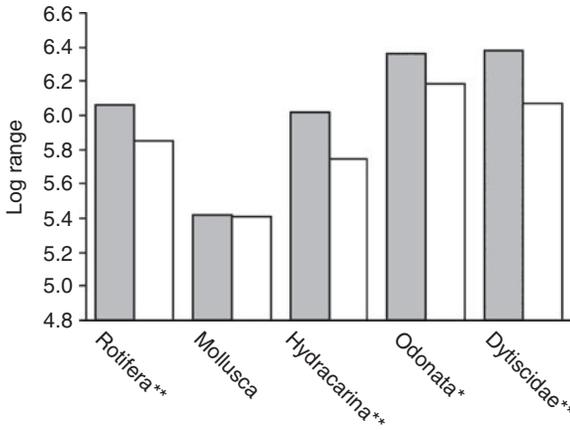
### Predictions at the species/population level

#### *Geographic range: overall size*

Our research into the different constraints that lotic and lentic habitats could impose on organisms originated from observations that, in the Iberian peninsula, most of the species of aquatic Coleoptera with narrow distributions were exclusively found in running waters (Ribera and Vogler, 2000). Using data on range sizes for 490 coleopteran species, we found that lotic species had much smaller distributional ranges than lentic species, and that the association of habitat type and range size had independently arisen in at least four monophyletic coleopteran lineages and several more times within each of these main groups. Similarly, Hof *et al.* (2006) found that lentic Northern hemisphere odonates had larger latitudinal spans, and more northern distribution centres and range boundaries, than lotic species. Although the data were collected for a different purpose, Monaghan *et al.* (2005) observed that Madagascan mayflies associated with small lentic water bodies had the larger ranges, and showed the most recent, and presumably most frequent, transoceanic colonizations. Analysis of Illies' (1978) data on west European freshwater invertebrates also showed that lentic species of Hydracarina, Rotifera and Dytiscidae, but not Mollusca, had larger average ranges than lotic species (Fig. 15.1) (Meyer, 2000).

#### *Geographic range: dynamics*

The most direct way to test whether lentic species experience more frequent and intense range shifts than lotic species would be to examine the fossil record. Preliminary analysis of Late Quaternary beetle data shows that most of the species in the families Dytiscidae and Hydraenidae experiencing range shifts (i.e. known

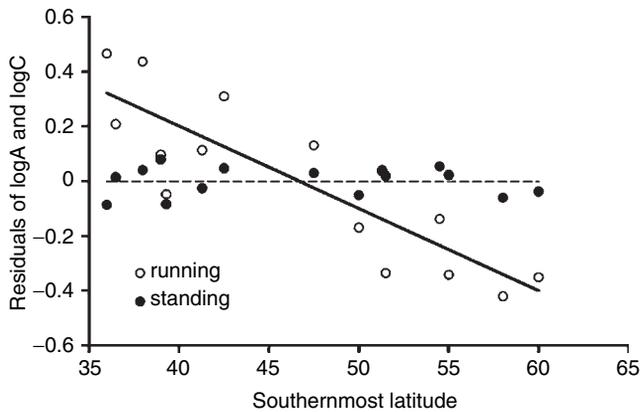


**Fig. 15.1.** Average range (in log km<sup>2</sup>) of lotic and lentic European species of five taxonomic groups (data from Illies, 1978, compiled by Meyer, 2000; see text and Table 15.3 for details). \*\* $P < 0.001$  in a two-tailed  $t$ -test comparison of averages; \* $P < 0.1$ .

as fossils from areas in where they do not currently occur) are mostly, or exclusively lentic (I. Ribera *et al.*, 2007 unpublished results). However, the fossil data has serious limitations, both temporal (covering in their vast majority only the last glacial cycle) and geographical (with virtually no records from the most species-rich areas in the Mediterranean). There are several other indirect ways of testing differences in range dynamics. In Ribera *et al.* (2001), two lineages of water beetles (family Dytiscidae) were compared: one with species living only in running waters (genus *Deronectes*), and one with species living only in standing water habitats (species of the *Ilybius subaeneus* group). Using species-level phylogenies, and assuming allopatric speciation, we tested the evolution of sympatry with node age: the prediction was that lotic species would keep allopatry longer than lentic species. When the degree of sympatry was plotted against relative node age, more allopatric splits were evident in the lotic *Deronectes*, suggesting a slower rate of range movement since speciation (medians of 0.5 and 0.8 in *Deronectes* and *Ilybius* respectively, where 0 is perfect allopatry and 1 fully overlapping ranges, Ribera *et al.*, 2001). However, differences were not significant when tested with the methodology of Barraclough and Vogler (2000).

Another set of predictions, derived from the greater hypothesized range movements of lentic species, pertain to latitudinal gradients and the different factors influencing the local and regional species richness of the two habitat types. Lentic species are expected to re-colonize recently glaciated areas faster than lotic species, the colonization success of the latter being more dependent on distance from glacial refugia. Ribera *et al.* (2003) collated species distributions for more than 800 species of water beetles in 15 regions across western Europe to test some of these predictions. Species number in any of these regions was related to three variables: total area, a measure of the geographic connectedness of the area and latitude. Pooled species numbers were, in general, accurately predicted based on these three simple measures (with correlations over 90% for the overall diversity), but correlations were different for lentic and lotic species. As predicted, lotic species were mostly correlated with latitude (as a surrogate of distance to refugia), while lentic species were only correlated with the measure of

connectedness or with area size (Fig. 15.2, Table 15.2). Again, these differences were also observed in each of the four phylogenetically independent lineages of aquatic Coleoptera when analysed separately. The number of species of the five groups studied in Meyer (2000) in each of the 17 areas defined in Illies (1978) show similar differences among running and standing water habitats (Tables 15.3, 15.4). For molluscs, dragonflies and diving beetles, the only variable significantly correlated to the number of lotic species was southernmost latitude. For water mites the number of lotic species was not related to any of the variables studied, and only for Rotifera was connectivity the most significant variable, while latitude was not significant (Table 15.4). On the contrary, lentic species of Rotifera, dragonflies and water mites were highly correlated with area and connectivity, but not latitude. For molluscs and diving beetles there was no significant correlation (at  $P < 0.05$ ) with any of the variables. Interestingly, the



**Fig. 15.2.** Relationship between the number of lotic and lentic species of aquatic Coleoptera in 15 areas in western Europe and the southern most latitude of these areas, after controlling for area (A) and 'connectivity' (C) (see text and Table 15.2 for details, data from Ribera *et al.*, 2003). The regression line is significant for lotic species ( $r^2 = 0.73$ ,  $P < 0.001$ ), but not lentic species ( $r^2 < 0.001$ ).

**Table 15.2.** Coefficients of determination ( $r^2$ ) from multiple regression of the logarithm of the number of species of aquatic Coleoptera in each of 15 areas in western Europe with three geographical variables; Area (in km<sup>2</sup>); southernmost latitude (sLatitude); and 'connectivity' (Con), a measure of the largest linear distance connecting each area with their neighbouring ones, intended to be a measure of the ease with which species could move through it.

Habitat	LogArea	sLatitude	LogCon	Combined	Sig.F
All	0.52	0.50	0.40	0.91	<0.00001
Running water	NS	0.56	NS	0.93	<0.000001
Standing water	NS	NS	0.84	–	<0.000001
Both	0.27	0.58	0.42	0.88	<0.0001

Sig. F indicates significance of variable based on an  $F$  test. Data from Ribera *et al.* (2003).

**Table 15.3.** The number of species, in five taxonomic groups, in 17 of the western European biogeographic areas defined in Illies (1978) (excluding islands and eastern areas with open boundaries), compiled by Meyer (2000).

No	Illies	Lat	Area	Con	Rotifera				Odonata				Mollusca				Dytiscidae				Hydracarina			
					R	S	B	T	R	S	B	T	R	S	B	T	R	S	B	T	R	S	B	T
1	1	36	689832	424	6	85	55	146	18	30	35	83	27	12	42	81	15	24	5	44	79	63	13	155
2	2	42.5	46768	424	3	42	34	79	9	18	28	55	20	7	35	62	14	17	1	32	63	28	8	99
3	3	38	227995	490	5	128	68	201	13	30	25	68	34	16	47	97	22	30	8	60	38	34	11	83
4	4	43	233841	953	27	184	100	311	14	37	30	81	39	17	46	102	18	31	4	53	147	86	21	254
5	5	42	175381	712	0	42	23	65	8	24	28	60	139	11	46	196	11	25	5	41	35	31	5	71
6	6	36.5	134459	307	1	47	35	83	10	24	31	65	40	82	45	167	13	20	4	37	41	22	6	69
7	7	40	192919	640	0	38	24	62	10	27	28	65	24	11	53	88	10	18	5	33	41	23	2	66
8	8	44	157843	751	6	82	51	139	13	35	29	77	30	10	43	83	14	28	4	46	100	61	18	179
9	9	48	292302	751	81	344	131	556	11	38	29	78	13	16	47	76	11	28	3	42	152	89	22	263
10	10	44.5	204611	738	34	221	98	353	8	37	29	74	16	12	44	72	5	21	2	28	140	21	11	172
11	11	44.5	192919	568	10	159	84	253	8	30	29	67	15	12	43	70	3	20	2	25	35	61	6	102
12	12	43.5	257225	1110	12	221	81	314	11	25	28	64	15	10	48	73	5	17	2	24	22	34	5	61
13	13	42.5	432606	914	10	150	75	235	17	30	27	74	28	14	49	91	15	36	6	57	79	85	19	183
14	14	50	572911	1130	61	412	137	610	9	38	30	77	9	16	48	73	7	32	3	42	75	148	23	246
15	15	53.5	227995	908	16	208	95	319	5	35	28	68	7	16	45	68	3	22	1	26	38	80	14	132
16	20	58	327378	496	5	149	62	216	3	22	0	25	5	13	34	52	4	22	2	28	19	43	7	69
17	22	60	280609	496	5	89	39	133	4	25	14	43	4	14	36	54	1	17	2	20	23	60	11	94

Species were categorized in running water (including springs, R), standing water (S) or both (B) according to the habitat preferences reported in Illies (1978). Illies = Number of the area as given in Illies (1978); Lat = latitude as measured at the southernmost point of the area; Area (in km<sup>2</sup>), estimated through image analyses methods; Con = Connectivity of the area (see Ribera *et al.*, 2003 for details).

**Table 15.4.** Significance of the regression between the number of species, in five taxonomic groups, in 17 of the western European biogeographic areas defined in Illies (1978) (excluding islands and eastern areas with open boundaries) and each of three geographical variables (data from Meyer, 2000; see Table 15.3). Species were categorized in running water (including springs, R), standing water (S) or both (B) according to the habitat preferences reported in Illies (1978).

Habitat	Taxa	Lat	logArea	logCon
logR	Dytiscidae	<0.01	NS	NS
	Hydracarina	NS	NS	NS
	Mollusca	<0.01	NS	NS
	Odonata	<0.01	NS	NS
	Rotifera	NS	<0.1	<0.01
logS	Dytiscidae	NS	<0.1	NS
	Hydracarina	NS	<0.05	<0.05
	Mollusca	NS	NS	NS
	Odonata	NS	<0.05	<0.05
	Rotifera	NS	<0.05	<0.01
logB	Dytiscidae	<0.05	NS	NS
	Hydracarina	NS	NS	NS
	Mollusca	<0.05	NS	<0.05
	Odonata	<0.01	NS	NS
	Rotifera	NS	<0.1	<0.05
logT	Dytiscidae	<0.05	NS	NS
	Hydracarina	NS	NS	<0.1
	Mollusca	<0.05	NS	NS
	Odonata	<0.05	NS	NS
	Rotifera	NS	<0.05	<0.01

Area (in km<sup>2</sup>) estimated through image analyses methods; Lat = latitude as measured at the southernmost point of the area; Con = Connectivity of the area (see Ribera *et al.*, 2003 for details).

only group in which lotic and lentic species show a similar pattern (i.e. no relation with latitude and both related with the measure of connectivity) was Rotifera, a group in which most species are good dispersers and have resistant forms (e.g. De Meester *et al.*, 2002). In any case, even for this group and using the same data set, lentic species have significantly larger ranges than lotic species (Fig. 15.1). The higher beta diversity of lotic species is a direct consequence of their smaller ranges and latitudinal gradient in species richness (Hubbell, 2001), and has been documented for European water beetles (Ribera *et al.*, 2003) and Holarctic dragonflies (Hof *et al.*, 2006).

#### *Genetic flow among populations*

Using a compilation of published allozyme data on more than 150 species of freshwater molluscs, insects and crustaceans from all over the world, Marten *et al.* (2006) analysed the genetic population differentiation of lentic and lotic species. They concluded that lentic invertebrates exhibit on average lower genetic population differentiation than lotic species, in a consistent way across the three studied

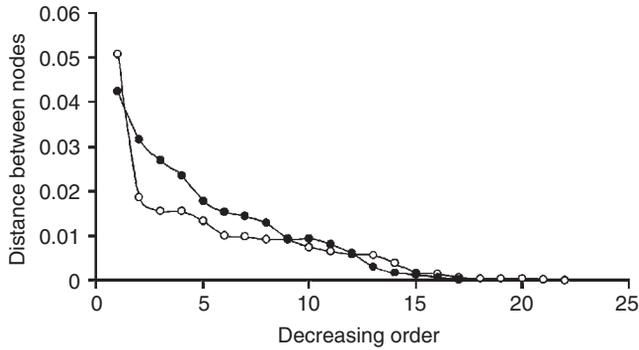
groups. Abellán *et al.* (2007) reported high levels of genetic divergence among populations of *Ochthebius glaber*, a species of Coleoptera exclusive to hypersaline running waters in south-east Spain. Although the comparative data were preliminary, nucleotide diversity within *O. glaber* was an order of magnitude higher (0.026 and 0.004, respectively) than a closely related species, *O. notabilis*, which is exclusive to hypersaline standing waters, despite the larger area occupied by populations of *O. notabilis* (from the Pyrenees to the south of the Iberian Peninsula).

## Predictions at the level of lineages

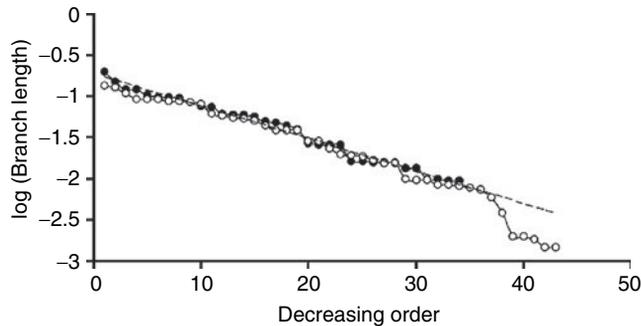
In the comparison of species-level phylogenies based on mitochondrial sequences for the lentic *Ilybius* and the lotic *Deronectes*, Ribera *et al.* (2001) found no significant difference in the lineage through time (LTT) plots of the linearized trees, intended to reflect the diversification pattern of a lineage (Barraclough and Nee, 2001). *Deronectes* displayed a higher frequency of recent splits than *Ilybius*, consistent with a higher evolutionary turnover and a higher frequency of recent species. The difference, however, was not significant compared with expected patterns under a constant speciation rate null model. Ribera *et al.* (2001) argued that current methods for analysing species-level phylogenies may not be powerful enough to discriminate contrasting cladogenetic patterns. A different possibility is that lentic and lotic clades may indeed display similar levels of species turnover, but the evolutionary processes take place at very different spatial scales—a Holarctic distribution for *Ilybius*, with some species spanning the whole realm, and a more restricted Mediterranean distribution for *Deronectes*, with abundant endemics with local distributions. In an attempt to find new approaches to compare cladogenetic processes based on linearized trees, I plotted both the distance between nodes in the LTT plot and the estimated length of the branches in decreasing order of magnitude. The distance between nodes in the *Ilybius* tree (lentic) follows an almost perfect logarithmic decrease, while the *Deronectes* tree shows a hollow curve with an excess of very large and small values (Fig. 15.3). This difference is not reflected in the standard deviation (0.01 in both cases), but in the kurtosis (10.4 and 0.6 for *Deronectes* and *Ilybius* respectively). The biological interpretation of the kurtosis is less straightforward than more commonly used statistics, but it can be taken as a measure of the high-level heterogeneity of the data (i.e. the way variance is distributed, Sokal and Rohlf, 1995).

The situation is similar when plotting the logarithm of the length of the branches (Fig. 15.4). The branches of the tree of *Ilybius* follow a linear trend, without apparent outliers, when plotted in decreasing order, suggesting that the logarithm of the time between cladogenetic events (as reconstructed in the phylogeny, i.e. with missing data and including extinctions) has a uniform random distribution. The distribution of branch lengths for the *Deronectes* tree is very similar, other than the presence of an excess of branches at the shorter end of the spectrum (Fig. 15.4). Again, this difference is mostly reflected in the kurtosis of the distribution: 7.4 for *Deronectes* and  $-0.2$  for *Ilybius*.

The results of the comparison of the distribution of branch lengths and inter-nodal distances in the LTT plots suggest a higher irregularity or unpredictability



**Fig. 15.3.** Distance between nodes in the lineage through time plot (LTT) of the linearized phylogenies of the genus *Deronectes* (lotic, white circles) and *Ilybius* (lentic, black circles), sorted in decreasing order (data from Ribera *et al.*, 2001). The distances between nodes in the lentic tree follows an almost perfect logarithmic decrease ( $r^2 = 0.99$ ), while those of the lotic tree have an excess of extreme high and low values ( $r^2 = 0.85$ ) (higher kurtosis, see text).



**Fig. 15.4.** Logarithm of the branches in the linearized phylogenies of the genus *Deronectes* (lotic, white circles) and *Ilybius* (lentic, black circles), sorted in decreasing order (data from Ribera *et al.*, 2001). The branch lengths in the lentic tree follow an almost perfect straight line ( $r^2 = 0.98$ ), while those of the lotic tree have an excess of extreme low values (higher kurtosis, see text).

of the cladogenetic processes in the lotic lineage. To what extent this is a general result, and if this can be taken as evidence of a higher evolutionary turnover, are still open questions.

## What's Next?

### Alternative explanations

Initial objections that could be levelled at the framework outlined in this chapter include the possibility of artefacts due to idiosyncratic factors of the groups studied,

or a biased distribution of habitat types in the studied areas. These types of alternative explanations lose strength when other geographical areas and taxonomic groups match the predictions (e.g. North American dragonflies, Hof *et al.*, 2006; Madagascan mayflies, Monaghan *et al.*, 2005; or a wide variety of aquatic macroinvertebrates, Meyer, 2000; Marten *et al.*, 2006). More difficult to address is the possibility that the factor driving the observed differences is not the contrasting long temporal stability of the habitat, but its ecological heterogeneity at shorter temporal scales. If lentic environments were ecologically more variable than lotic habitats at temporal scales much smaller than the lifespan of some organisms (e.g. daily variations on temperature, oxygen concentration; or seasonal variations in water level, amount of vegetation, temperature, etc.), the need to withstand wider ecological conditions may result in a wider geographical range (a similar mechanism to that used by Stevens, 1989, to explain Rappoport's rule). Once differences in the size of the geographic range are established, some of the processes detailed above will start to take place and, consequently, the observed patterns will also be similar (Dynesius and Jansson, 2000; Harley *et al.*, 2003; Jablonski and Roy, 2003; Qian and Ricklefs, 2007).

Under this alternative scenario, there does not need to be any difference in dispersal ability. Consequently, there should be no differences in genetic geographical structure among populations at the same geographical scale, and latitudinal gradients should not be related to post-glacial colonization. While the presence of latitudinal gradients could be related indirectly to ecological tolerance (Stevens, 1989), the observation of clear differences in the genetic structure of populations at the same geographic scale does not seem to support this interpretation. These two possibilities (differences in ecological heterogeneity at short temporal scales and differences in long-term stability) are compatible and it is possible that both may contribute, in a different proportion depending on the circumstances, to the global patterns reported here.

### The paradox of the 'living-dead'

If the scenario outlined here is accurate, species living in running waters have similar characteristics to those considered 'super specialists': reduced size of the geographical range, genetic isolation and fragmentation of populations, and high probability of extinction. When habitat characteristics are kept through successive cladogenetic events (either for phylogenetic inheritance or *de novo* habitat constraints due to a specific geographical setting), the question becomes how could these lineages survive despite the high probability of extinction, i.e. why do old running-water clades occur at all? Other than by chance (given enough of them, some will survive), an obvious possibility is the regular renewal of the clade by the appearance of a widespread lotic species, which could start a new cycle of differentiation and fragmentation (and eventually extinction). It is important to remember that the habitat constraints are not symmetrical: while lentic species *have to* move when the habitat disappears, lotic species *do not need* to move that frequently. Thus, while among lentic species the frequency of outliers (i.e. species with small ranges) is expected to be low, within lotic lineages it is not

rare to find widespread species (Ribera and Vogler, 2000). The possibility exists that these widespread lotic species act as 'diversity pumps', extending the range of existing clades and keeping a constant supply of new species, in a similar case to the 'taxon cycle' or 'taxon pulse' (e.g. review in Liebherr and Hajek, 1990). The situation will be similar to that described by Janz *et al.* (2006) with butterflies, in which high diversity may be kept through cycles of range expansion by host switching and subsequent diversification by fragmentation. Specialization alone cannot generate diversity as it is only a 'pruning' process; to generate diversity, consecutive cycles of generalists (by incorporating new hosts) and subsequent specialization would be necessary (Janz *et al.*, 2006). The question remains as how these 'generalist' (i.e. widespread) species appear in the first place, that is, how the constraints that act on most species in the same habitat (so that patterns are highly significant statistically) are not relevant in some particular cases.

Disregarding the possibility of taxonomic artefacts, there are different possibilities as to why a lotic species may have a widespread geographic range.

(i) *Ecological particularities*. Some taxa may be tied to particular microhabitats, or habits, that select for high dispersal abilities, even if they are usually found within a general lotic setting. For example, some of the species traditionally considered as 'aquatic' are in fact riparian. Among aquatic Coleoptera, this is the case with many species of Dryopoidea that have widespread distributions despite being exclusively associated with running waters (e.g. there are no presently recognized Iberian endemics among Limnichidae, Heteroceridae or Dryopidae). It is likely that riparian species are constrained by different factors than those affecting true aquatic species (e.g. most of them are good fliers, with very good dispersal abilities).

(ii) *Relative age of the species*. There may be a 'species life cycle', with young species originating in a small area, dispersing to reach a maximum stable distribution and then contracting again on the way to extinction (e.g. Taylor and Gotelli, 1994; Gaston, 1994, 2003; Webb and Gaston, 2000; Vrba and DeGusta, 2004; Foote *et al.*, 2007). Under this scenario, the average shorter duration of lotic species would be a contributing factor to their smaller ranges, as they would have little time to reach their full potential distribution. Species that, for any reason, escape extinction could reach a wider geographical range.

If this was the case, young species will have restricted distributions around their centre of origin, 'mature' species will have widespread distributions and old species will have restricted relict distributions, not necessarily close to their centre of origin. To distinguish between restricted distributions around the centre of origin and relict distributions (in the sense of remains of a former wider geographical range), the relative geographical position of the species in the clade could be studied. It is expected that, in species remaining in their centre of origin, geographically close species will also be phylogenetically close. On the contrary, species with relict distributions will not necessarily have their closest relatives in geographically close areas.

(iii) *Privileged geographical position*. In the Western Palaearctic, widespread lotic species tend to have a central and north European distribution, i.e. including the areas most affected by the Pleistocene glaciations. Among the water beetles,

in these areas there are few, if any, species with restricted distributions (Ribera *et al.*, 2003). Two main hypotheses have been put forward to account for this pattern.

First, the Mediterranean as a refuge (e.g. Hewitt, 2000): During the glacial maxima, the populations of most European species were confined to refuge areas in the southern peninsulas, from where they would have re-colonized the continent in the interglacials. The flow of migration would be mostly south to north, with southern peninsulas acting as a 'melting pot' in which genetic diversity is maximal, and northern populations being a subset of the southern genetic diversity. Widespread species will be those that could re-colonize Europe after the glaciations; species with restricted distributions, those that would remain in one of their refuges, having (for any reason) being unable to re-expand.

Second, the Mediterranean as an area of endemism (Bilton *et al.*, 1998; Ribera and Vogler, 2004): Rather than a source of re-colonizers, the southern peninsulas are a source of endemism: the isolation during the glacial cycles was enough to prevent genetic flow among the peninsulas and mainland Europe. These southern endemics would not re-colonize the European mainland, but remain confined as species with restricted distributions in the southern areas. The flow of migration was mostly east–west, rather than north–south. Only the species/populations in the areas at the edge of the southern peninsulas (e.g. Pyrenees, Alps, Carpathians) would be able to expand their ranges to the north, with most of the species/populations in the south being isolated and genetically homogeneous, but distinct from those in mainland Europe. Widespread species will be those that remained in, or next to, mainland Europe; species with restricted distributions those that were geographically isolated in the southern peninsulas.

Under the first scenario, the genetic diversity of the southern populations of the widespread species will be maximal, and the species with restricted distribution will not follow a clear geographical pattern (i.e. species geographically close will not necessarily be phylogenetically close). Under the second scenario, the genetic diversity of the widespread species does not need to be larger in the southern populations, and species with restricted distributions will have a clear geographical pattern (phylogenetically close species will be geographically close).

(iv) *Differences in the ecological tolerance of the species.* Species with restricted distributions may have a limited physiological tolerance, whereas widespread species may be able to cope with a wider range of environmental or habitat conditions. To be considered an explanation of the differences in the size of the geographical range of closely related species, the physiological differences must precede the range expansion of the widespread species, and not result from a subsequent adaptation to the local conditions. The range of the widespread species also has to be ecologically and climatically more diverse than that of the species with restricted distributions.

(v) *Stochastic processes.* Gaston and He (2002) found that a stochastic null model fits several range size distributions well, so the question is whether there is even a pattern to explain. Given enough species, and assuming there is some variance in the distribution of size ranges, there will always be some widespread species among lotic lineages that, on average, may still have much smaller ranges than their lentic counterparts.

## Further Work

Although most evidence so far supports the model presented here, there are areas in need of further study. The most prominent among them is perhaps to test some of the macroecological patterns in less well-studied southern areas, as well as in a wider range of macroinvertebrates. Obvious candidates, for which enough information is available for several groups, include Australia, Southern Africa or austral South America. The study of the same groups (e.g. aquatic Coleoptera) will allow the direct comparison with areas in the northern hemisphere, but the inclusion of other groups will allow wider conclusions – especially if there are differences among them that could be interpreted in terms of differences in ecology, life cycle or other biological characteristics.

Some of the straightforward predictions of the model are untested, although in many cases work is in progress. Thus, the Quaternary beetle record offers an untapped possibility of comparative studies, despite the limitations outlined above. Similarly, the wealth of descriptive methods to model distributions and potential niches could be used to compare the match between potential and realized niches in lotic and lentic species, or to introduce habitat as a predictive factor in models of global change or habitat alteration.

More complex are tests of the predictions of differences in the probability of habitat shifts, and in the evolutionary turnover of lineages. In the later case, it is expected that this high turnover will leave a signal in both the topology of the tree and the distribution of branch lengths or internodal distances (as measured with LTT plots), but these are notoriously difficult to characterize and to compare in a statistical framework (see above). Simulations are a potential powerful tool for these kind of comparisons, although the risk exists of oversimplification, which could lead to a decrease in statistical power.

There is also the problem of how to integrate differences in geographical scale in the comparison of phylogenetic trees. When confined to the same geographical space, the prediction is that two lineages of contrasting habitat types will develop according to the model outlined here. However, if space is not a limiting factor, the outcome may be less clear: the genetic/evolutionary processes may result in the same topological or diversification patterns, but at very different geographical scales (Ribera *et al.*, 2001). More specifically, it could be that two species have the same metapopulation dynamics over their whole range, with a given level of geographic isolation among populations, amount of genetic variation and geographic structure, as measured, for example, by haplotype distribution and divergence, degree of isolation by distance, etc. In a scale-less geographical matrix, both species may be indistinguishable when looking only at haplotype trees, networks or other measures of population genetic structure, but may have contrasting absolute sizes of the geographical range—which implies that, if confined to a similar space, both would have very different dynamics.

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