

Scale-dependence of the correlation between human population and the species richness of stream macro-invertebrates

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Abstract

Recent biogeographical studies have shown positive correlations between plant/vertebrate species richness and human population presence. The same pattern has been reported for Ephemeroptera (mayflies), Plecoptera (stoneflies) and Trichoptera (caddisflies) (EPT) amongst European countries. This is surprising as EPT are bio-indicators of stream pollution and most local studies report higher species richness of these macro-invertebrates where human influences on water quality are lower. Using a newly collated taxonomic dataset, we studied whether the species richness of EPT is related to human population size at finer resolutions (Italy's regions, provinces and $10 \times 10 \text{ km}^2$ UTM cells) controlling for sampling effort, variations in area and for spatial autocorrelation. At all study grains, observed EPT species richness was strongly correlated to the number of records available for the same taxon. At the regional level, the observed number of Ephemeroptera and Plecoptera species significantly increased with increasing human population size. At the provincial level, observed species richness decreased significantly with increasing human population size for Ephemeroptera and did not vary significantly for Plecoptera and Trichoptera. At the finest grain scale, there were significant negative correlations of observed Ephemeroptera and Trichoptera species richness with human population size, although the proportion of variance explained was very low. These results were broadly confirmed when analyzing the estimated number of species using the formula of Chao2. Our analysis confirms the scale-dependence of the human population–biodiversity correlation. Over broad scales more populated regions tend to have more species than less populated ones. Restricting the study grain, the positive EPT species–people relationship disappears and turns into a negative one. Our findings suggest a challenge also for the conservation of regional EPT diversity.

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Zusammenfassung

Neuerliche biogeografische Untersuchungen haben positive Korrelationen zwischen dem Artenreichtum von Pflanzen bzw. Wirbeltieren und der Anwesenheit menschlicher Populationen gezeigt. Das gleiche Muster wurde für

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Ephemeroptera (Eintagsfliegen), Plecoptera (Steinfliegen) and Trichoptera (Köcherfliegen) (EPT) in europäischen Ländern gezeigt. Dies ist überraschend weil EPT als Bioindikatoren für Verschmutzungen gelten und die meisten lokalen Untersuchungen einen höheren Artenreichtum dieser Makroinvertebraten dokumentieren wenn der menschliche Einfluss auf die Wasserqualität geringer ist. Unter Nutzung eines neuerlich zusammengetragenen Datensets untersuchten wir, ob der Artenreichtum der EPT mit der menschlichen Populationsgröße bei feinerer Auflösung (Italiens Regionen, Provinzen und $10 \times 10 \text{ km}^2$ UTM Abschnitte) in Beziehung steht und kontrollierten Beprobungsaufwand, Variation der Fläche und räumliche Autokorrelationen. Bei allen Auflösungen der Untersuchung war der beobachtete Artenreichtum der EPT stark mit Anzahl der verfügbaren Erfassungen für jedes Taxon korreliert. Auf der regionalen Skala nahm die Artenzahl der Ephemeroptera und Plecoptera signifikant mit einer zunehmenden menschlichen Populationsgröße zu. Auf der Provinzebene nahm der beobachtete Artenreichtum bei den Ephemeroptera mit zunehmender menschlicher Populationsgröße signifikant ab und zeigte keine signifikante Variation bei den Plecoptera und Trichoptera. Auf der kleinsten Skala gab es signifikante negative Korrelationen zwischen dem beobachteten Artenreichtum der Ephemeroptera und Trichoptera und der menschlichen Populationsgröße, obwohl der Anteil der erklärten Variation sehr gering war. Diese Ergebnisse wurden weitgehend durch die Analyse der geschätzten Artenzahlen nach der Formel von Chao2 bestätigt. Unsere Ergebnisse bestätigen die Skalenabhängigkeit der Korrelation zwischen Biodiversität und menschlicher Population. Auf großen Skalen tendieren stärker besiedelte Regionen dazu mehr Arten zu haben als geringer besiedelte Gebiete. Bei einer Beschränkung des Untersuchungsrahmens verschwindet die positive EPT-Menschen-Beziehung und verwandelt sich in eine negative. Unsere Ergebnisse stellen zudem eine Herausforderung für den Erhalt der EPT-Diversität dar.

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Introduction

A positive correlation between species richness and human population presence is now commonly reported (Luck, 2007). This correlation is at first sight counter-intuitive, as biodiversity could be thought to be higher in less densely populated and thus still semi-natural regions, but can be explained by the preferential settlement of human beings in regions with high environmental productivity and/or habitat heterogeneity, which in turn are species-rich regions. This broad-scale co-occurrence is relevant for conservation, because the many detrimental local impacts of human beings on biodiversity are magnified if species-rich regions are more densely populated.

Positive broad-scale species–people relationships are now known for most continents (Hunter & Yonzon, 1993; Fjeldså, 2007; Knapp, Kühn, Klotz & Schweiger, 2008). The range of taxa involved in these studies has been mainly limited to plants and vertebrates, but a positive large-scale species–people correlation can apply also to invertebrates such as butterflies, aphids and grasshoppers (Luck, Ricketts, Daily & Imhoff, 2004; Steck & Pautasso, 2008; Pautasso & Powell, 2009). Surprisingly, a positive species–people correlation has also been reported for bio-indicators of water quality (Ephemeroptera, Plecoptera and Trichoptera: EPT) amongst European countries (Pautasso & Fontaneto, 2008).

EPT are common bio-indicators of freshwater biotic integrity (Ode, Rehn & May 2005). Given their habitat

requirements and sensitivity to disturbance, the species richness of EPT tends to be lower in streams with higher human impacts (Figueroa, Valdovinos, Araya & Parra, 2003; Dinakaran & Anbalagan, 2007). These impacts include watercourse and floodplain alteration, the related enhanced erosion, industrial and sewage waste (Fochetti & de Figueroa, 2006; Martel, Rodriguez & Berube, 2007). Therefore, it could be expected that EPT might be an exception to the positive large-scale species–people correlation. The report of a positive correlation between EPT species richness and people for European countries (Pautasso & Fontaneto, 2008) prompts the questions of (i) how general this pattern is for EPT, and whether it persists (ii) at a narrower scale of analysis and (iii) when controlling for sampling effort.

This study aims to answer these three questions. We investigate whether there is a species–people correlation for EPT in Italy's regions, provinces and 100 km^2 cells, thus at a much finer study grain and over a more restricted study extent than for European countries. Although Italy is a species-rich European country from the point of view of EPT, Italian investigations of stream macro-invertebrate diversity in relation to environmental parameters and human activities have only been patchy (DiGiovanni, Goretti & Tamanti, 1997; Ravera, 2001; Lucadamo, De Filippis, Mezzotero, Vizza & Gallo 2007). Moreover, the data available allow us to control for variations in sampling intensity and to study whether sampling intensity is correlated with human population presence.

Methods

Observed and estimated species richness for the orders Ephemeroptera, Plecoptera and Trichoptera in Italy's 20 regions, 102 provinces and 3556 UTM ($10 \times 10 \text{ km}^2$) squares were based on the checklist and distribution of the Italian fauna database (Ruffo & Stoch, 2005). This is a recently compiled nation-wide collection of faunistic records. The average year of the EPT records is 1986, 1979 and 1982, respectively. But records reach to the days of the last national human population census (the latest year of the EPT records is 1999, 1999 and 2004, respectively).

The human population size for 2001 and the area of Italian regions and provinces (which are completely nested levels) were obtained from the Italian National Institute of Statistics (ISTAT). The human population size for 2001 of the UTM squares was obtained from the Corine database of the European Union (smallest mapping unit = 25 ha). For the range and average values of human population and areas of Italy's regions and provinces, see Pautasso & Chiarucci (2008). The maximum human population size for the UTM squares was 1,123,000 (Milano, Lombardy), the average ca. 5000, and the median ca. 6200. There were 34 UTM squares without inhabitants.

The database had 6055 records of 102 Ephemeroptera species (mean = 59 records per species; median = 18 records per species), 4705 records of 153 Plecoptera species (mean = 31 records per species; median = 19 records per species), and 13181 records of 425 Trichoptera species (mean = 31 records per species; median = 9 records per species; see Appendix A). The national coverage of the dataset for the EPT species present in Italy is adequate, as the *Fauna Europaea* (2004) reports 96, 142 and 359 EPT species for mainland Italy (which excludes the two main islands Sicily and Sardinia). According to the *Fauna Europaea* (2004), Italy is the most species-rich country in Europe for Trichoptera representing 33% of European fauna, the second for Plecoptera (33%), and the sixth for Ephemeroptera (28%).

Estimated species richness was calculated using Chao's bias-corrected formula (Chao 2) (Chao, 1984, 2005). Chao's estimated species richness is based on the number of singletons and doubletons (species recorded once and twice). Chao's estimator has been shown to give similar results to other commonly used estimators (Hortal, Borges & Gaspar, 2006; Muirhead, Ejsmont-Karabin & Macisaac, 2006). For regions, estimated species richness was calculated from the recorded species at the single sites, not for the cumulative species lists in provinces.

We ran multi-variate General Linear Models (GLMs) of EPT species richness as a function of human population size controlling for variations in number of

records and, for regions and provinces, in area. Variations in number of records were controlled for as a co-variate in the multi-variate models, both for observed and for estimated species richness. We then analysed whether number of records was correlated with human population size and/or region/province area. Number of EPT species and records, human population size, and area were log-transformed to conform to the assumptions of statistical tests. For the UTM squares, only those with EPT occurrences were retained in analyses. Ideally, the database would contain EPT records from all UTM cells. Unfortunately, the higher the resolution, the higher the amount of zeros, i.e. empty cells. However, there seems to be little bias in terms of human population size for UTM cells with presence of EPT (see Appendix A). Moreover, in order to control for potential bias in Chao's estimates owing to a low number of records per UTM cell, we repeated the analysis disregarding the UTM cells with a number of records below the arbitrary threshold of 10.

Analyses were carried out in SAS 9.1. Spatial autocorrelation was controlled for using mixed models with exponential co-variance structure (Pautasso, 2007). Spatial models retained the same predictors of the GLMs described before. Spatial models are more robust because they take into account a potential spatial non-independence of data points close to each other in terms of species presence, survey intensity, and environmental parameters, which can otherwise lead to misleading parameter estimates (e.g. Dormann, 2007, but see Hawkins, Diniz-Filho, Bini, De Marco & Blackburn, 2007, and the Online Appendix A). Apart from the proportion of variance explained (which refers throughout to non-spatial models) we present only the results of the spatial models.

Results

At the regional level, observed species richness increased significantly with increasing human population size when controlling for area and number of records for Ephemeroptera and Plecoptera, but not for Trichoptera (Table 1). In all cases, observed species richness was strongly positively related to the number of records of the same taxon and not significantly related to region area. There was no significant relation between the number of EPT records and either human population size or region area (Table 2).

At the provincial level, again controlling for area and number of records, the observed species richness of Ephemeroptera decreased significantly with increasing human population size (Table 1). There were no significant variations of observed Plecoptera and Trichoptera species richness with human population size

Table 1. Mixed models of the species richness (log spp) of Ephemeroptera (E), Plecoptera (P), and Trichoptera (T) in Italy's regions ($n=20$), provinces ($n=102$), and in the UTM cells (100 km^2) with occurrence of these taxa in the dataset used ($n=697$ (E), 569 (P), and 1196 (T)) as a function of human population size (log pop), area (for regions and provinces only; log area) and number of records (log rec). For Trichoptera in provinces, results are of the non-spatial model (the spatial model did not converge). Parameter estimates are given with their standard errors; p values are in parentheses.

Grain	Taxon	AIC	r^2	Log spp =	log pop	log area	log rec
Reg	E	-7.3	0.77	-0.19	+0.32±0.14 (0.04)	-0.26±0.23 (0.29)	+0.30±0.07 (0.004)
	P	-13.9	0.78	0.59	+0.17±0.08 (0.05)	-0.30±0.16 (0.08)	+0.47±0.05 (0.0001)
	T	-17.8	0.64	0.46	+0.06±0.08 (0.44)	+0.02±0.16 (0.91)	+0.38±0.05 (0.0001)
Prov	E	-88	0.91	0.83	-0.10±0.05 (0.04)	-0.04±0.06 (0.52)	+0.63±0.02 (0.0001)
	P	-107	0.95	0.36	-0.00±0.04 (0.94)	-0.11±0.06 (0.06)	+0.77±0.02 (0.0001)
	T	-	0.93	0.41	-0.01±0.04 (0.86)	-0.03±0.05 (0.56)	+0.67±0.02 (0.0001)
UTM	E	-1158	0.93	0.13	-0.02±0.01 (0.002)		+0.82±0.01 (0.0001)
	P	-1333	0.98	0.03	-0.004±0.005 (0.32)		+0.91±0.06 (0.0001)
	T	-2544	0.97	0.06	-0.007±0.004 (0.06)		+0.87±0.01 (0.0001)

Table 2. Mixed models of the records of species (log rec) of Ephemeroptera (E), Plecoptera (P), and Trichoptera (T) as a function of human population size (log pop) and area (for regions and provinces only; log area) in Italy's regions (reg; $n=20$), provinces (prov; $n=102$), and in the UTM squares with presence of these taxa ($n=697$ (E), 569 (P), and 1196 (T)). Parameter estimates are given with their standard errors; p values are given in parentheses.

Grain	Taxon	AIC	r^2	log rec	Log pop	log area
Reg	E	35.1	0.30	-1.89	+0.72±0.45 (0.13)	-0.10±0.83 (0.91)
	P	36.4	0.08	-0.36	+0.03±0.41 (0.93)	+0.57±0.75 (0.46)
	T	25.6	0.13	0.54	-0.37±0.34 (0.29)	+1.08±0.63 (0.10)
Prov	E	185	0.10	-0.98	-0.09±0.19 (0.65)	+0.82±0.23 (0.001)
	P	215	0.15	-2.98	-0.12±0.22 (0.58)	+1.42±0.27 (0.001)
	T	182	0.18	-1.05	-0.18±0.19 (0.36)	+1.10±0.23 (0.001)
UTM	E	941	0.00	0.56	+0.03±0.03 (0.31)	
	P	851	0.02	0.98	-0.11±0.03 (0.0004)	
	T	1883	0.01	1.00	-0.08±0.02 (0.001)	

of provinces. In all cases, observed species richness was strongly positively related to the number of records of the same taxon and not significantly related to province area. There was a significant positive relation between the number of EPT records and province area, and

no significant relation with human population size (Table 2).

At the 100 km^2 level, the observed species richness of Ephemeroptera decreased significantly with increasing human population size when controlling for number of

records (Table 1). There were no significant variations of observed Plecoptera species richness with human population size of UTM squares and a marginally significant decline of observed Trichoptera species richness. There was a significantly negative relation between the number of records and human population size of UTM squares for Plecoptera and Trichoptera, although the proportion of variance explained was negligible (Table 2).

These results were broadly confirmed when analyzing the estimated EPT species richness using Chao's formula. At the regional level, there were significant increases of estimated species richness with increasing human population size for Ephemeroptera and Plecoptera, and a marginally significant increase for Trichoptera (Fig. 1A, D, G). When controlling for the number of records, the relationship was significant only for Ephemeroptera (Table S1). At the provincial level, there were no significant variations in estimated EPT species richness with human population size, either on its own (Fig. 1B, E, H) or controlling for area and number of records (Table S1). At the UTM level there were significant decreases in the estimated species richness of Plecoptera and Trichoptera with increasing human population size (Fig. 1C, F, I). However, this was not the case when controlling for the number of records

(Table S1). In this case, there was a marginally significant decline of estimated species richness with increasing human population size for Ephemeroptera.

When restricting analyses to UTM cells with at least 10 EPT records, for all taxa, both for observed and estimated species richness, and both when controlling for the number of records or not, we did not find significant variations in species richness as a function of human population size. We note that this restriction to at least 10 records greatly reduces the dataset in all three cases (Ephemeroptera: 29%, Plecoptera: 22%, and Trichoptera: 31% of UTM cells with records of these taxa). Therefore, even if in this case the data are more reliable because of the higher number of records, they are hardly comparable with the whole dataset because the majority of UTM cells with records of species is left out of the analyses.

Discussion

The biodiversity of freshwater ecosystems is declining rapidly (Clarke, MacNally, Bond & Lake, 2008). These ecosystems are in fact held to be just as threatened as tropical rainforests (Ricciardi & Rasmussen, 1999).

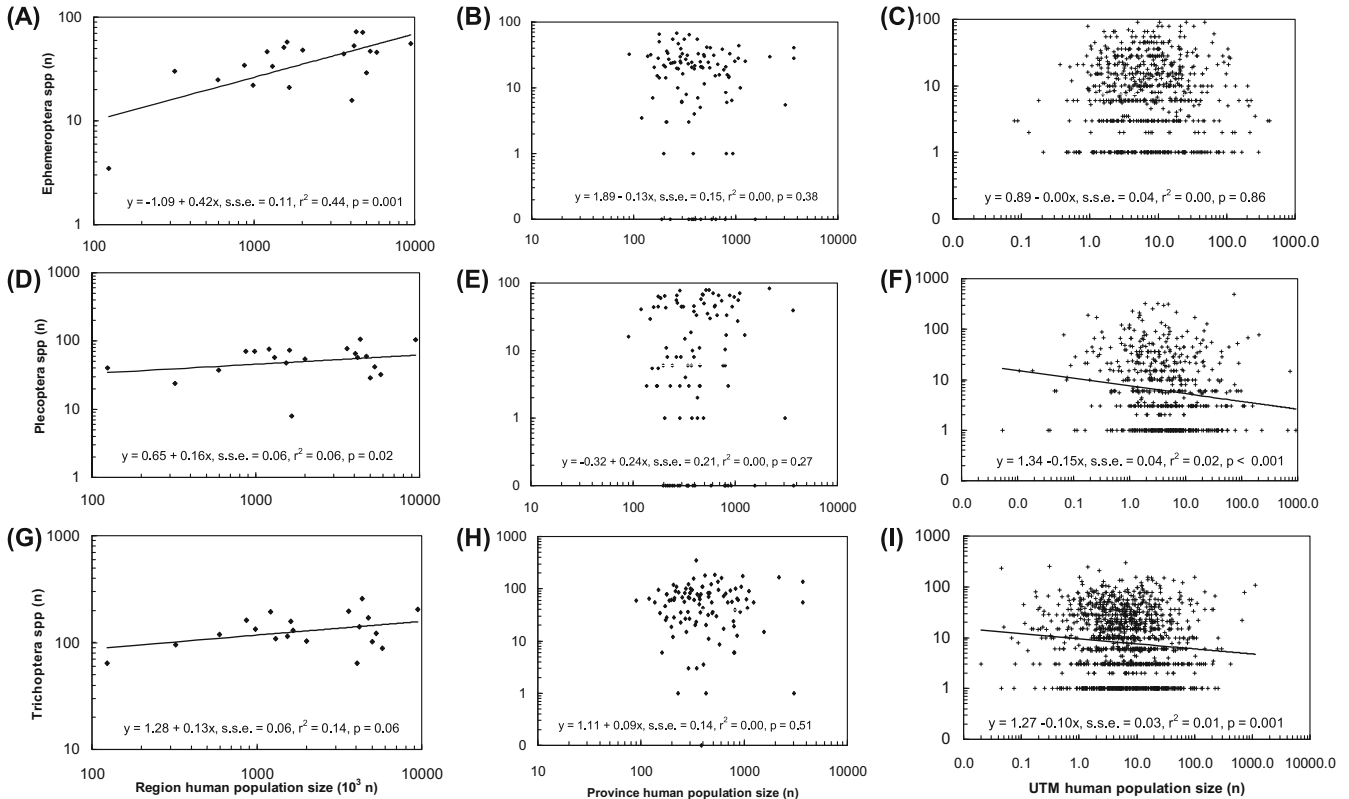


Fig. 1. The relationship between estimated Ephemeroptera (A, B, C), Plecoptera (D, E, F) and Trichoptera (G, H, I) species richness (Chao) and human population size (from the 2001 census) in Italy's (A, D, G) 20 regions, (B, E, H) 102 provinces and (C) the 697, (F) 569 and (I) 1196 UTM squares ($\sim 100 \text{ km}^2$) with presence of these taxa. Log–log scale, s.s.e = slope standard error.

World-wide, EPT genera richness is correlated with measures of net primary productivity (Winson & Hawkins, 2003). Assuming that also for Italian stream macro-invertebrates genera and species richness are positively correlated (as has been shown for other taxa, e.g. Balmford, Green & Murray, 1996) and assuming that also in Italy human population size is positively correlated with energy availability, this can explain why, at least over broad scales, EPT diversity matches human population size.

The spatial co-occurrence of high numbers of stream macro-invertebrate species and of human beings over regional scales is a challenge for conservation. This follows from the detrimental effects of urbanization and other human activities, which can lead to biodiversity loss and homogenization (Kühn & Klotz, 2006; Strayer, 2006). Italy is part of the Mediterranean hotspot of biodiversity, is a relatively densely populated country which has been modified by human beings for a long time and thus provides a good example of the high threat currently experienced by Mediterranean ecosystems (Underwood, Viers, Klausmeyer, Cox & Shaw, 2009). Our findings highlight the importance of the scale of ecological studies when drawing conclusions for environmental policy (Allan, Erickson & Fay, 1997; Boyero, 2003; Mykrä, Heino & Muotka, 2007).

The positive correlation between EPT species richness and human population size reported for European countries (Pautasso & Fontaneto, 2008) is confirmed for Italy's regions for Ephemeroptera and Plecoptera, but not for Trichoptera. Even for Ephemeroptera and Plecoptera, the correlation is at the boundary of statistical significance. This result confirms that with decreasing grain and extent the species–people correlation tends to weaken (Hardy & Dennis, 1999; Pautasso & Chiarucci, 2008). However, when analyzing the estimated species richness, the regional species–people relationships show highly significant p values at least for Ephemeroptera and Plecoptera.

At the provincial level, the species–people correlation is not significant for Plecoptera and Trichoptera, and is significantly negative for Ephemeroptera (but the significance disappears for estimated species richness). At the $10 \times 10 \text{ km}^2$ level, the most local grain in this analysis, there are significant negative correlations with human population size of Ephemeroptera and Trichoptera species richness, although the proportion of variance in species richness explained by human population size is low and most of the variation in species richness is associated with the number of records available. These findings confirm that at intermediate scales (between regional and local) the positive species–people correlation tends to disappear. The pattern already starts to reverse for Ephemeroptera at the provincial scale of analysis, even though the mean province area is 3000 km^2 , and for Ephemeroptera and

Trichoptera at the grain size of 100 km^2 . These results are further evidence for a scale-dependence of the species–people correlation and suggest that the boundary between a positive species–people correlation over broad scales and negative correlation at a more restricted scale of analysis could be different for invertebrates compared to vertebrates (Luck, 2007; Pautasso, 2007), or to terrestrial compared to freshwater ecosystems (Lassalle, Crouzet & Rochard, 2009).

It has been suggested that in some cases the general relationship between species richness and human population size may be an artefact, due to a more thorough knowledge of species occurrences in more populated regions (e.g. Luck, 2007). Our analysis rules out this possibility for the data analyzed, as the positive species–people correlations of Ephemeroptera and Plecoptera at the regional level hold true when controlling for the number of records in the database. In addition, at this grain of analysis, the number of EPT records is not significantly correlated with human population size. This lack of evidence for the hypothesis that variations in sampling intensity may explain a positive EPT species–people correlation for Italy confirms the reliable knowledge of regional EPT species occurrences in Europe (Barber-James, Gattolliat, Sartori & Hubbard, 2008; de Moor & Ivanov, 2008; Fochetti & de Figueroa, 2008). At the $10 \times 10 \text{ km}^2$ level, we even document a negative correlation between number of records and human population size, at least for the cells with presence of Plecoptera and Trichoptera, which suggests that, locally, these taxa tend to be more often studied away from human settlements. For Plecoptera this is confirmed by the significantly higher human population size of UTM cells with presence of data compared to cells without data, although also in this case the proportion of variance in human population size explained by the presence or absence of Plecoptera records is low.

Remarkably, estimated species richness (which is supposed already to take into account variations in sampling effort) is generally still correlated with the number of records. This result is interesting in its own right. It is possible that fieldworkers may preferentially sample regions, which they expect to have more species. Alternatively, the correlation of estimated species richness and number of records could be explained by a general under-sampling of Italy from the point of view of EPT. Additional systematic EPT data are thus required to further investigate patterns in the biodiversity of stream macro-invertebrates across Italy.

The data currently available suggest that, together with a higher number of species of ancient trees (Pautasso & Chiarucci, 2008), macrofungi (Pautasso & Zotti, 2009) and birds (Pautasso & Dinetti 2009), more populated Italian regions have a higher number of Ephemeroptera and Plecoptera species than less

populated ones. Therefore, most Italian people live in regions with a high biodiversity, also of macro-invertebrates. Since these taxa are bio-indicators of water quality, our findings show that more populated Italian regions still contain sub-regions with relatively low human impacts. However, at the more local level there is no longer a positive species–people correlation, and a negative one appears for Ephemeroptera, and in part for Trichoptera. This means that the negative impacts of human beings on freshwater ecosystems already start to be perceived at a relatively coarse grain size.

The proportion of variance in EPT species richness explained by human population size at the UTM level is very low. However, the correlations are highly significant. Moreover, in large-scale analyses of biodiversity (with data coming from different observers and many confounding factors) it is common to observe such low r^2 values. For example, the r^2 of the species–area relationship for the living collections of the botanic gardens in the world is 0.05. A similar value has been found for the species–people correlation for introduced soil macro-invertebrates in North America north of Mexico (Lilleskov, Mattson & Storer, 2008). It is possible that more substantial r^2 values may be found when analyzing the EPT species–people correlation at even finer resolutions. However, the $10 \times 10 \text{ km}^2$ grid cell is the finest grain size the database allows us to use. It is already interesting to study this correlation at these three grain sizes, as there is evidence that a positive large-scale species–people correlation is starting to turn into a negative one at a more local scale, also given the many previous reports of a negative influence of human beings on the species richness of macro-invertebrates at local scales. For EPT assemblages, such a negative direct influence of local human activities has been widely documented (Kerans & Karr, 1994; Malmqvist, 2002), so that these assemblages have become biological tools commonly used in environmental assessment (Friberg et al., 2006; Park et al., 2007; Blocksom & Johnson, 2009).

Using EPT as tools for assessing biological quality in streams within the Water Framework Directive of the European Community (Steyaert & Ollivier, 2007; Skoulikidis, Karaouzas & Gritzalis, 2009) will need to take into account that EPT species richness varies consistently not only among countries, but also within countries at the regional level. Future efforts to restore river health (Palmer, Allan, Meyer & Bernhardt, 2007) should allow for potential variation in EPT species richness amongst European regions and should take into account the scale-dependence of the species–people correlation. Ideally, such efforts would also need baseline knowledge of EPT species richness prior to human disturbance. Given that the regional pool of species can be an important determinant of the success of river

restoration measures, also large-scale EPT biodiversity should be object of conservation. Further work is needed to examine how the scale-dependence of the EPT species–people correlation fits with variations in features of watercourses such as width, volume and pollution. If detailed spatial information about the presence of water treatment plants were available, it would be interesting to take also the effect of this factor in consideration. A regional EPT species–people positive correlation, the intensification of land use, habitat fragmentation, reshaping of watercourses banks and the increasing abandonment of marginal land are major impediments for the achievement of the goal of halting biodiversity loss in Europe by 2010.

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Appendix A. Supplementary material

The online version of this article contains additional supplementary data. Please visit [10.1016/j.baae.2009.09.005](https://doi.org/10.1016/j.baae.2009.09.005).

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