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On neutral metacommunity patterns of river basins at different scales of aggregation

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[1] Neutral metacommunity models for spatial biodiversity patterns are implemented on river networks acting as ecological corridors at different resolution. Coarse-graining elevation fields (under the constraint of preserving the basin mean elevation) produce a set of reconfigured drainage networks. The hydrologic assumption made implies uniform runoff production such that each link has the same habitat capacity. Despite the universal scaling properties shown by river basins regardless of size, climate, vegetation, or exposed lithology, we find that species richness at local and regional scales exhibits resolution-dependent behavior. In addition, we investigate species-area relationships and rank-abundance patterns. The slopes of the species-area relationships, which are consistent over coarse-graining resolutions, match those found in real landscapes in the case of long-distance dispersal. The rank-abundance patterns are independent of the resolution over a broad range of dispersal length. Our results confirm that strong interactions occur between network structure and the dispersal of species and that under the assumption of neutral dynamics, these interactions produce resolution-dependent biodiversity patterns that diverge from expectations following from universal geomorphic scaling laws. Both in theoretical and in applied ecology studying how patterns change in resolution is relevant for understanding how ecological dynamics work in fragmented landscape and for sampling and biodiversity management campaigns, especially in consideration of climate change.

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1. Introduction

[2] Understanding local and regional patterns of species distributions is a major goal of ecological and biological research [Levin, 1992; Nilsson *et al.*, 1994; Matthews, 1998; Levine, 2000a, 2000b, 2003; Rodriguez-Iturbe *et al.*, 2009]. Ecological systems are complex and seemingly unpredictable because of the large number of interacting individuals of different species involved, but patterns in the spatial distribution of organisms provide important clues about the underlying mechanisms that structure ecological communities. Although many mechanisms governing the biodiversity of species have been described, we are far from a complete understanding of the factors controlling the probabilistic properties of ecological patterns. Also it is not clear either what ecological descriptors can be assumed as invariant across different scales of observation and resolutions, or the

interactions between geomorphological features and ecological dynamics, in this context hinged to river network structure. Similarity across spatial scales remains an open issue in ecological research where most studies focus on variables across a specific level of observation. Frequently, predictions from numerical models are available at resolutions coarser than those typical of ecological investigations [Levin, 1992]. Many of these studies refer to one particular species [Green *et al.*, 2004; Green and Bohannan, 2006] with the extension to multispecies ecosystems being far from trivial. In this paper, we address these issues for ecosystems in fluvial dendritic networks that obey the neutral theory [Hubbell, 2001]. Biodiversity patterns, especially those of vegetation, may have effects of such ecosystem functions as productivity, nutrient cycling, and sediment transport; these functions in turn affect hydrological processes like evapotranspiration and runoff production. Furthermore, understanding the linkage between geomorphology and ecology in fragmented fluvial ecosystems is an relevant topic [Benda *et al.*, 2004], especially toward biodiversity preservation in response to climate change or anthropic interventions. Indeed an important problem in theoretical and applied landscape ecology is understanding whether and how biodiversity patterns change as a function of what is actually measured. Here the null hypothesis is the resolution invariance of biodiver-

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sity patterns facing the established such features of fluvial landscapes [Rodríguez-Iturbe and Rinaldo, 1997].

[3] Space fragmentation plays a larger role in river basins than in savannas ecosystems since in the first case the drainage network acts as a stronger controlling factor for the spreading of organisms [e.g., Nilsson *et al.*, 1989; Gascon *et al.*, 2000; Honnay *et al.*, 2001; Levine, 2003; Rodríguez-Iturbe *et al.*, 2009]. Interactions have also been documented among hydrogeomorphological features of nondendritic landscapes and ecological patterns. For examples in savannas where a preferential connectivity is not exerted by a network, Caylor and Shugart [2006], Scanlon *et al.* [2007], and Borgogno *et al.* [2009] documented the existence of power laws on the size of the vegetation clusters, an important feature explained through local interaction mechanisms acting under a global hydrologic constrain. Power law clusters of halophytic vegetation have also been documented by Marani *et al.* [2004] for tidal environments where hydrologic controls are provided by tidal networks whose geomorphological features [Marani *et al.*, 2002, 2003] differ from fluvial ones. As for river basins in water-controlled ecosystems it appears there may exist mechanisms leading to the optimal organization of vegetation patterns around the channel network structure under the controlling influence of water stress [Caylor *et al.*, 2004, 2005]. Other empirical studies have suggested the importance of the river network on the biodiversity of freshwater fish, and in general of riverine habitats [Poole, 2002; Ward *et al.*, 2002; Wiens, 2002; Fernandes *et al.*, 2004; Benda *et al.*, 2004; Fisher *et al.*, 2007; Muneeppeerakul *et al.*, 2008a]. It has been found, for instance, that fragmentation within river networks may produce long-term genetic variations among species and communities [Colwell, 2000; Gascon *et al.*, 2000]. As ecological corridors, river networks also affect the spreading of human population and of waterborne disease [Rodríguez-Iturbe *et al.*, 2009]. Also in the case of river basins, Muneeppeerakul *et al.* [2008b] made clear the crucial effect that directionality, a key feature for certain species living in the drainage network ecosystem, has on biodiversity patterns.

[4] With the above premises, the present paper specifically aims at investigating, under general coarse graining of the networked landscape: the resolution invariance of species-area relationships; the interplay between the network shape and the dispersal of species; and the behavior of relevant macroecological descriptors, like species richness at local and regional scale and pairwise species similarity, through different scales of spatial aggregation. The embedded constraint in river basins is that the dispersal of species may happen only along the directed spanning structure of the drainage network that exhibits clear scale and resolution invariant properties over several orders of magnitude [Rodríguez-Iturbe and Rinaldo, 1997]. In general patterns of species richness in real landscapes may differ from the neutral ones addressed in this study [Chave *et al.*, 2002; Purves and Pacala, 2005], therefore it is accepted that even in the presence of strong species-specific interactions neutral models may capture broad features of biodiversity patterns.

[5] The metacommunity model is built around four main assumptions.

[6] 1. The simulations are performed on space-filling networks (i.e., all the pixels are channelized), implying

there is no differentiation between hillslope and channel sites. The only geomorphological constraints are thus provided by drainage directions.

[7] 2. We assume that each stream link, defined as the portion of channel between two consecutive confluences (in turn dependent on a threshold for the size of tributary), constitutes one local community (LC).

[8] 3. All the local communities have the same habitat capacity, the number of individuals in each local community. The implicit assumption here is that the climatic variation over the studied region is negligible. Then the hydrologic assumption is that the runoff production is the same for all the links, which implies the habitat capacity is uniform in space.

[9] 4. Neutrality implies that each individual is competitively equivalent at per capita level regardless of species [Hubbell, 2001]. The neutral theory is a valid approximation considering species at the same tropic level that equally interact like particles. Neutral theory is capable of generating patterns of abundance, diversity, species turnover, and geographic range similar to those observed in natural ecosystems that in fact do not feature neutral relationships among species [see, e.g., Bell, 2001; Purves and Pacala, 2005; Mouillot and Gaston, 2007; Muneeppeerakul *et al.*, 2008a].

[10] The paper is organized as follows. Section 2 introduces the river basins used in the study, explains the essential concepts of the coarse-graining (CG) procedure and defines the geomorphological quantities employed in the analysis. Section 3 describes the neutral metacommunity model, with explicit reference to the assumptions it involves. Section 4 presents the main results while section 5 presents a comparative analysis of three different networks, as well as a discussion and perspectives for future works.

2. On Coarse-Graining River Basins

[11] Both real river basins as well as theoretical constructs are studied in this paper, namely, the Cordevole and Tanaro basins in northern Italy, and an optimal channel network (OCN) in a square lattice domain [Rodríguez-Iturbe *et al.*, 1992]. The latter is an artificial network obtained through a selection process minimizing total energy dissipation (a property of steady state landforms) from which one obtains scaling forms that are in excellent agreement with real networks extracted from DEMs [e.g., Rodríguez-Iturbe and Rinaldo, 1997]. The river networks extracted from the real basins and the OCN are plotted in Figure 1. Details on the Cordevole and Tanaro basins are given by Convertino *et al.* [2007]. Digital elevation models (DEMs) are employed in order to derive elevation maps at different scales of aggregation, or resolutions, from which the space-filling networks are extracted (see Figure 1). Note that a space-filling network is obtained when all pixels in the landscape domain are assumed to be channelized. In the case at hand, the DEM of Cordevole river basin has a drainage area of 691 km² (255 × 271 pixels at a resolution of 100 m), and the Tanaro river basin has a drainage area of 530 km² (178 × 296 pixels at a resolution of 100 m). The planar optimal channel network (OCN) is generated via a simulated annealing process which minimizes the total dissipation of

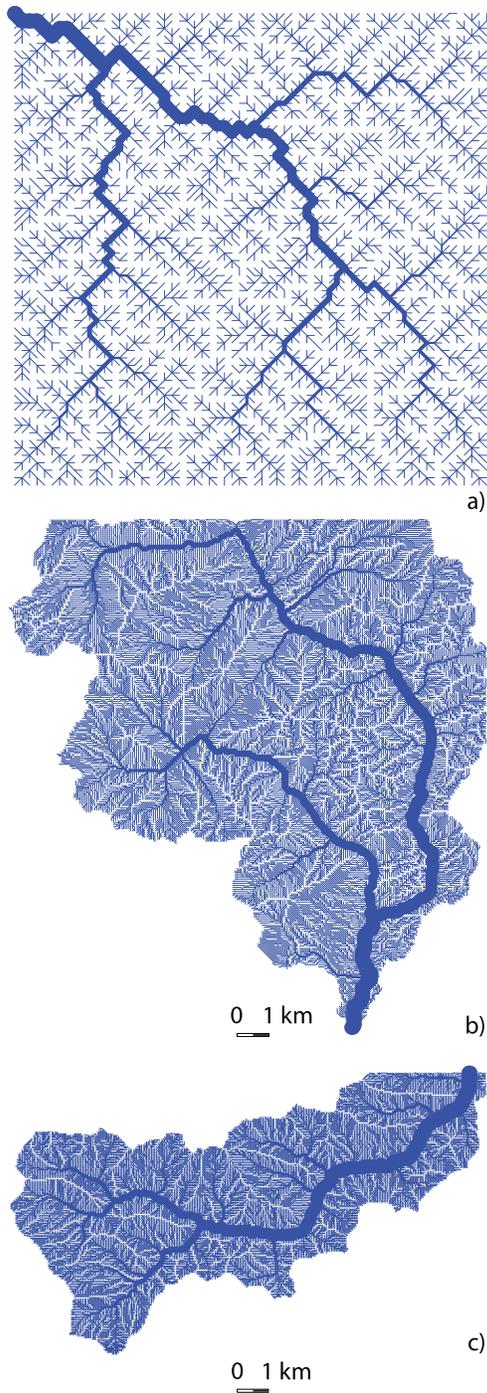


Figure 1. Space-filling networks derived from DEMs at their original finest resolution: (a) OCN with single outlet and no flux on sides, whose overall dimensions are 66×66 pixels (each of which is arbitrarily assumed to correspond to an area of $100 \times 100 \text{ m}^2$); (b) Cordevole, main tributary of Piave basin, northern Italy, suitably extracted from the DEM, 255×271 pixels, at 100 m resolution; (c) Tanaro, Po basin, northern Italy, extracted from the DEM, 178×296 pixels at 100 m resolution. The space-filling character is enforced by a threshold area for channelization $A \geq A_{th} = 1$ in pixel units.

energy expenditure in the transport of water. The chosen dimensions are 66×66 pixels, corresponding to a drainage area of approximately 44 km^2 where an arbitrary resolution of 100 m is assumed for comparative purposes with the real river basins. The associated 3-D landscape of the OCN is derived using the slope-area relationship $|\nabla z_i| \propto A_i^{\gamma-1}$ with $\gamma = 0.5$, where $|\nabla z_i|$ is the elevation gradient and z_i the elevation of each pixel with drainage area A_i [e.g., *Rodríguez-Iturbe and Rinaldo, 1997*].

[12] The dependence on the resolution of observation of the biodiversity patterns is studied by observing how they vary upon coarse graining in the description of the river basin. Figure 2 illustrates the coarse-graining procedure applied to the Tanaro river basin. An example of invariance of geomorphological properties across different resolutions is shown in Figure 3 for the three basins, where the probability of exceedance of the drainage area $P(A \geq a)$ at a randomly chosen point is plotted at different scales of aggregation. The distribution of A is maintained across different resolutions, although the accuracy of the estimation of the slope in the scaling region decreases under coarse graining. The elevation of an arbitrary pixel i at a certain resolution λ is given by the mean value of the elevations z_i of pixels at the finest resolution encompassed in the area $\lambda^2 \delta^2$ of the new pixel i , where δ is the side length at the finest resolution and λ the resolution parameter (see Figure 2). The invariance law of the cumulative drainage areas throughout the coarse-graining operation (Figure 3) is a direct consequence of the fractal structure of the river basin [*Rodríguez-Iturbe and Rinaldo, 1997*]. It is important to note that across CG resolutions the potential energy of the landscape is kept constant, and although the general directions of the fluxes are similar across CG resolutions, the connectivity of the network experiences changes.

[13] We now define several geomorphological quantities that will be used throughout the following sections. A stream link, as introduced in the hypothesis in section 1, is defined as the link connecting a pixel i to another pixel j where no tributaries occur between them. If a confluence is encountered a new stream link originates. The diameter, ϕ_i , is defined as the average distance from the stream link i to all other stream links j in the network, where the distance is measured through the network. As defined above, it is a measure of the degree of connectivity associated with a stream link and it is crucial for the dispersal dynamics in a river network. While the diameter is usually specified as the longest path between any pairs of links in the network [e.g., *Newman, 2003*] the definition of an ecological diameter as stipulated above seems more appropriate to our scope. Figure 4 shows the spatial patterns of the diameters for the river basins under study. Note that the minimum diameter, ϕ_{\min} , is farther away from the outlet in the Tanaro river basin than in the OCN and the Cordevole. Moreover, link diameters do not necessarily change monotonically with their distance from the outlet. This is due to the elongation of the river basin, defined as the ratio between its longitudinal and transversal characteristic lengths, say L_{\parallel} and L_{\perp} , respectively (Figure 2). The more elongated the network is, the closer to the middle of the basin the stream link with minimum diameter, ϕ_{\min} , tends to be. The elongation is a characteristic that is likely to be important in the functioning of river networks as ecological

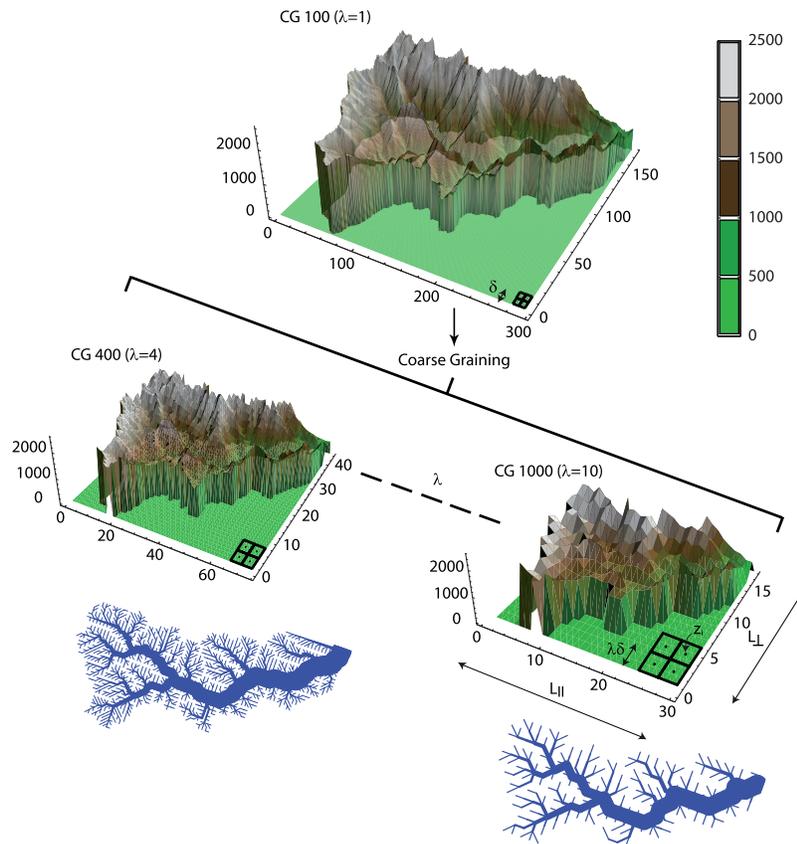


Figure 2. Illustration of coarse-graining (CG) technique applied to derive different elevation fields of the Tanaro basin starting from (top) the most detailed DEM ($\lambda = 1$), whose extracted network is shown in Figure 1. Although coarse graining brings changes into how stream links are connected, which in turn modifies the slope-area relationship of the original landscape, the obtained CG DEMs still statistically preserve the slope-area scaling relationship. L_{\perp} and L_{\parallel} are the transversal and longitudinal diameters of the basin. All CG landscapes are derived from the original topography with $\lambda = 1$ by averaging the elevations of λ^2 neighboring pixels. Here $\delta = 100$ m is the pixel size at the original resolution. Extracted networks and CG DEMs are shown for (bottom) CG = 400 ($\lambda = 4$) and CG = 1000 ($\lambda = 10$). The mean elevation is preserved across aggregation scales.

corridors. Notice that the average value of the diameter of the network, that is reported in each plot, corresponds to the average distance between stream links.

3. Neutral Metacommunity Model on River Networks

[14] This study makes use of the neutral metacommunity model developed by *Muneeppeerakul et al.* [2008a] for freshwater fish biodiversity. In this framework, the system is made up by different local communities with a certain habitat capacities, interconnected through the ecological corridors provided by the river network. No life history optimal survival strategies are accounted for in our model.

[15] Variables and parameters employed in the model are summarized in the Notation section. The analysis of results is done after the system reaches stationarity when the stochastic variable S_T , i.e., the number of species in the whole basin, is stable. At each time step, a random individual in a random local community (LC), i.e., a link in the space-filling network, dies and its site becomes available for

colonization. With probability ν , the per site diversification rate, this site will be colonized by a species not already present in the system; with the remaining probability $1 - \nu$, the site is colonized by a propagule of an individual already existing in the system. The per site diversification rate, ν , is given by the ratio θ/N , where θ is the overall diversification rate (or biodiversity parameter [Hubbell, 2001]), that is, the average number of new species introduced at each generation, and N is the total number of individuals in the system.

[16] We investigate a number of biodiversity patterns, to be described in section 4, after the system has reached the stationary state where the total number of species in the system, S_T , fluctuates within a narrow range and the ecological patterns observed no longer show systematic variations. A statistically stationary value of S_T is achieved on average at the same simulation time regardless of the ecological scenario implemented, the basin and the resolution. We proceed as follows for the three basins: (1) generation of the networks at the four different CG resolutions, (2) run the model to the stationary state for the four CG resolutions, and (3) analysis of macroecological patterns emerging from

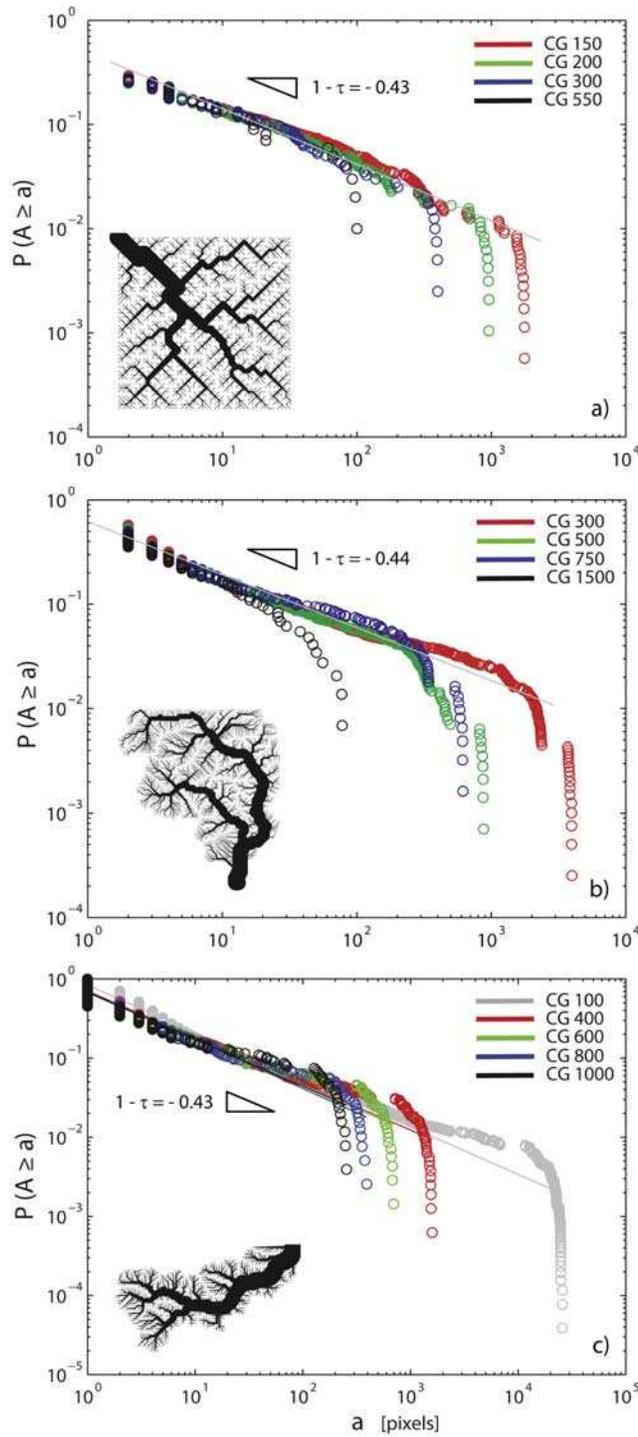


Figure 3. Probability of exceedance $P(A \geq a)$ of the drainage area in pixel units at any randomly chosen point, A , for the (a) OCN and the (b) Cordevole and (c) Tanaro river basins, using different levels of coarse-graining CG. The scaling exponents are very close to the typical value for river basins $1 - \tau = 0.43$: the reported average over resolution and the standard errors (Table 3) are found by reduced major axis regression. The value a_{\max} , i.e., scenario a at the outlet, decreases because a_i is characterized here by the number of links upstream of site i . The resolution parameter λ is given by the coarse-graining resolution divided by the finest resolution in meters, i.e., $CG/100$.

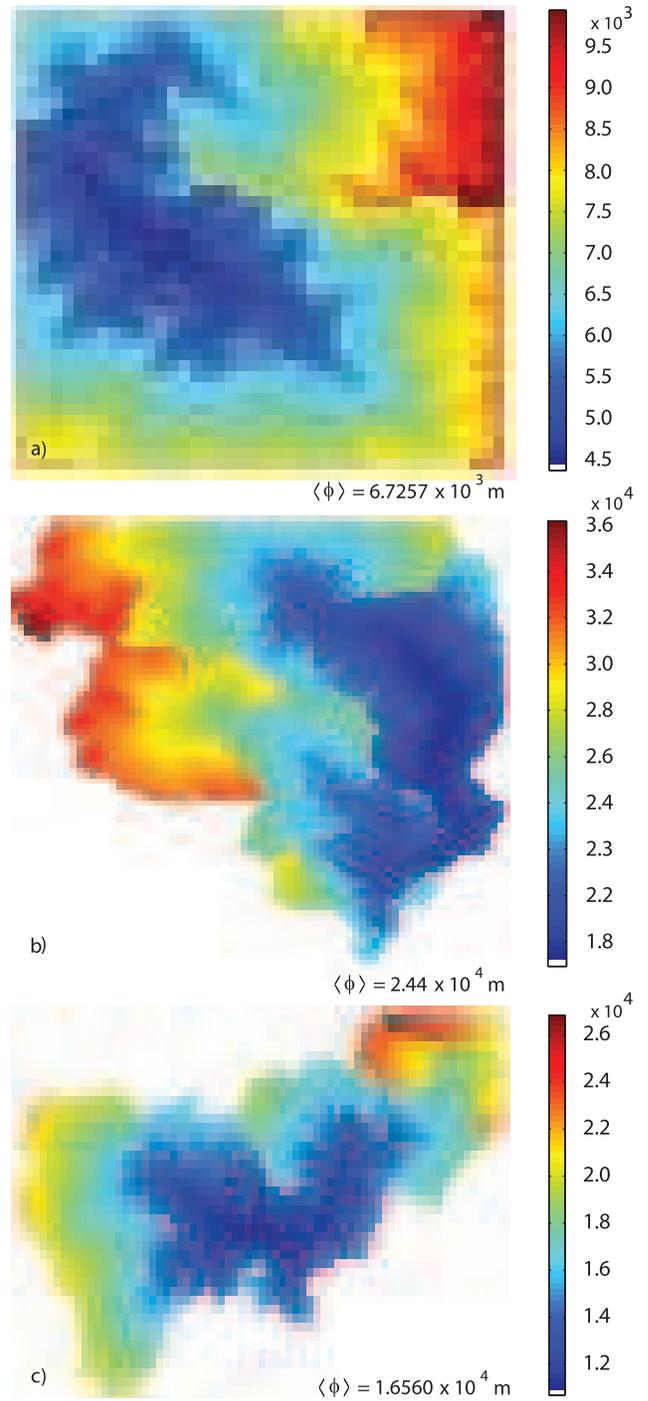


Figure 4. Spatial patterns of the stream link diameters for the (a) OCN and (b) Cordevole and (c) Tanaro basins, shown at CG = 150, 300, and 400, respectively. The diameter ϕ_i is defined as the average length from the stream link i to all other stream links j in the network.

each resolution. The probability P_{ij} that an empty site in link i is colonized by an individual from link j is given by

$$P_{ij} = \frac{K_{ij}H_j}{\sum_j K_{ij}H_j}, \quad (1)$$

where K_{ij} is the dispersal kernel (see below) and H_j is the habitat capacity of link j , assumed to be uniform and

Table 1. Total Number of Links and Habitat Capacity at Link Scale Across Coarse-Grained Scales for the Three Basins Under Study^a

CG	OCN				Cordevole				Tanaro			
	150	200	300	550	300	500	750	1500	400	600	800	1000
<i>n</i>	1711	924	383	96	2755	1036	478	114	1208	546	308	217
<i>H</i>	58	108	261	1042	36	97	209	877	82	183	325	461

^aHere *n* is the total number of links and *H* is the habitat capacity at link scale. The total habitat size, *N*, and the diversification rate, θ , are kept constant and equal to 1×10^5 and 40, respectively, in all cases. CG resolutions for all networks are derived from original DEMs at pixel resolution 100×100 .

constant for all links. H_j is given by the ratio N/n between the total number of individuals N (kept constant under coarse graining) and the number of links n that depends on the coarse graining level adopted. Therefore n decreases from the finest to the coarsest resolution. Table 1 gives the values of n and H employed for all the river networks and the different coarse-graining levels used in this paper. See Table 2 for the numerical values of the parameters assumed in the simulated ecological scenarios.

[17] The dispersal kernel K_{ij} represents the probability that a propagule produced at a site j arrives at i after dispersal. The general kernel structure implemented in this paper is given by

$$K_{ij} = C \left[\exp\left(-\frac{L_{ij}}{d_l}\right) + \frac{b^2}{L_{ij}^2 + b^2} \right], \quad (2)$$

where C is a normalization constant determined numerically such that, $\sum_i K_{ij} = 1$ for every local community j (i.e., individuals do not travel out of the system, which is assumed to be isolated), where N is the total number of communities. The kernel used herein is a combination of an exponential (with mean dispersal length d_l , when $b = 0$) and Cauchy distributions which adds a fat tail character to K_{ij} [Muneepeerakul *et al.*, 2008a]. The ecological distance L_{ij} is defined as the length of the shortest path from link j to link i through the network. Distances are measured in meters, rather than in pixel or link units, allowing for proper comparisons across different coarse-graining levels. The middle point of each stream link is used for calculating the distances used in the kernel, as well as for the calculation of the diameter and the distance between links. In the case $b = 0$ the structure of the kernel is exponential. If $b > 0$, the kernel is a combination of the exponential and the Cauchy components and exhibits a fat tail that produces a long-distance dispersal. In the first case equation (2) decays exponentially instead. In the latter case it has a power law decay that implies higher probability to have the same species at larger distances L_{ij} . Notice that, it is under the latter hypothesis that the model of Muneepeerakul *et al.* [2008a] better describes the pattern of fish biodiversity in the Mississippi-Missouri river system.

[18] As for the details of interactions depending on the fine spatial scales in stream links, consistently with a neutral metacommunity approach, we assume that they may be well summarized by using finite local habitat capacities. Ulti-

mately, this rests on the limited availability of local resources and turns out to be a plausible assumption under stationary conditions. On the other side, here we are describing an isolated ecosystem which evolves on temporal scales smaller than those characteristic of the actual speciation. Therefore, one expects that the temporal variations in the diversification rates are negligible. Nonetheless here we focus on the effect of resolution change solely.

[19] In the following, we shall refer to two different ecological scenarios implied by different structures of the dispersal kernel: the exponential case (scenario a) and the exponential-Cauchy case (scenario b). The different sets of parameters are given in Table 2.

4. Biodiversity Patterns of River Basins at Different Scales of Resolution

[20] This section focuses on the dependence of different biodiversity measures on the spatial resolution for the networks used in the analysis (OCN, Cordevole, Tanaro). The two different ecological scenarios with parameters given in Table 2 are implemented for all river networks at different coarse graining levels. All results presented here are the ensemble average over ten snapshots after the system has reached a statistically stationary state. For the biodiversity patterns analyzed (Figures 5, 6, 7, 8, 9, and 10), the lowest coefficient of determination is 0.78, computed by using the standard deviation averaged over ten realizations at stationary state. The deviation of each single-realization curve from the average over the ten snapshots is small and for this reason we have reported only the mean curve for the patterns analyzed. The coefficient of determination, R^2 , has been reported for the SAR because it is very consistent upon coarse graining.

[21] First, we have analyzed the rank-abundance (RA) curves resulting from the two ecological scenarios, namely the exponential and exponential-Cauchy dispersal kernel case for the three basins (Figures 5a, 5c, and 5e and 5b, 5d, and 5f, respectively). Here, the abundance of a species is simply the number of individuals belonging to that species. In both cases, the plots show overlapping curves from different coarse grain levels. In addition, we investigated the RA curves as a function of the dispersal parameters d_l and the diversification rate θ . The resolution invariance of the RA curves is not observed only for very local dispersal. Under such circumstances, in fact, the influence of the dispersal, and therefore that of coarse graining, is stronger on the total number of species. It is interesting to note that the number of species at the steady state, S_T , significantly depends on the dispersal only when d_l values are small independently of the diversification rate; this is in agree-

Table 2. Values of the Parameters Used in the Neutral Metacommunity Model for the Three Ecological Scenarios as Defined in the Text^a

Case	d_l	b	θ	N
Scenario a	500	0	40	1×10^5
Scenario b	500	300	40	1×10^5

^aFor brevity we refer to scenario a as the exponential case and to scenario b as the exponential-Cauchy case.

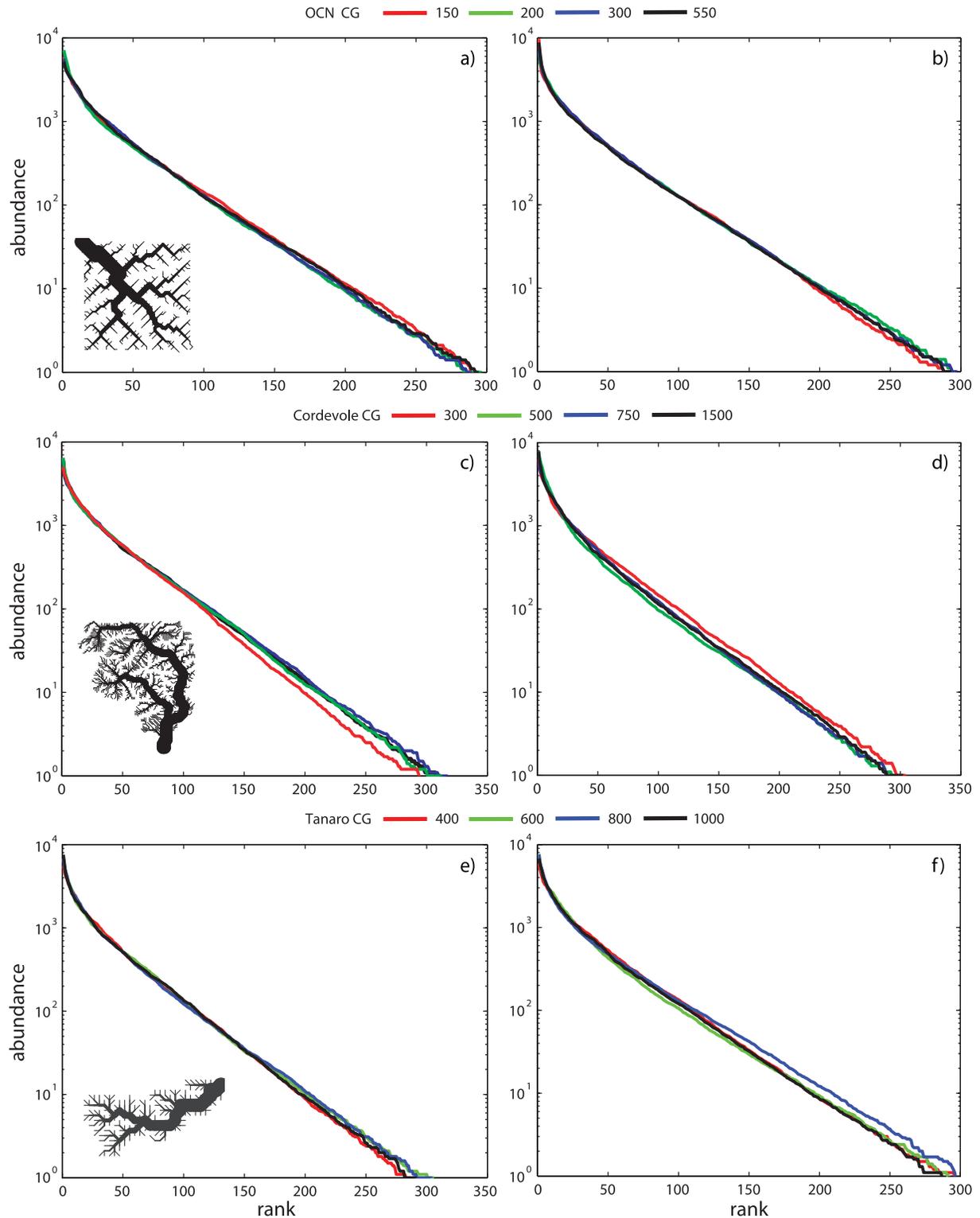
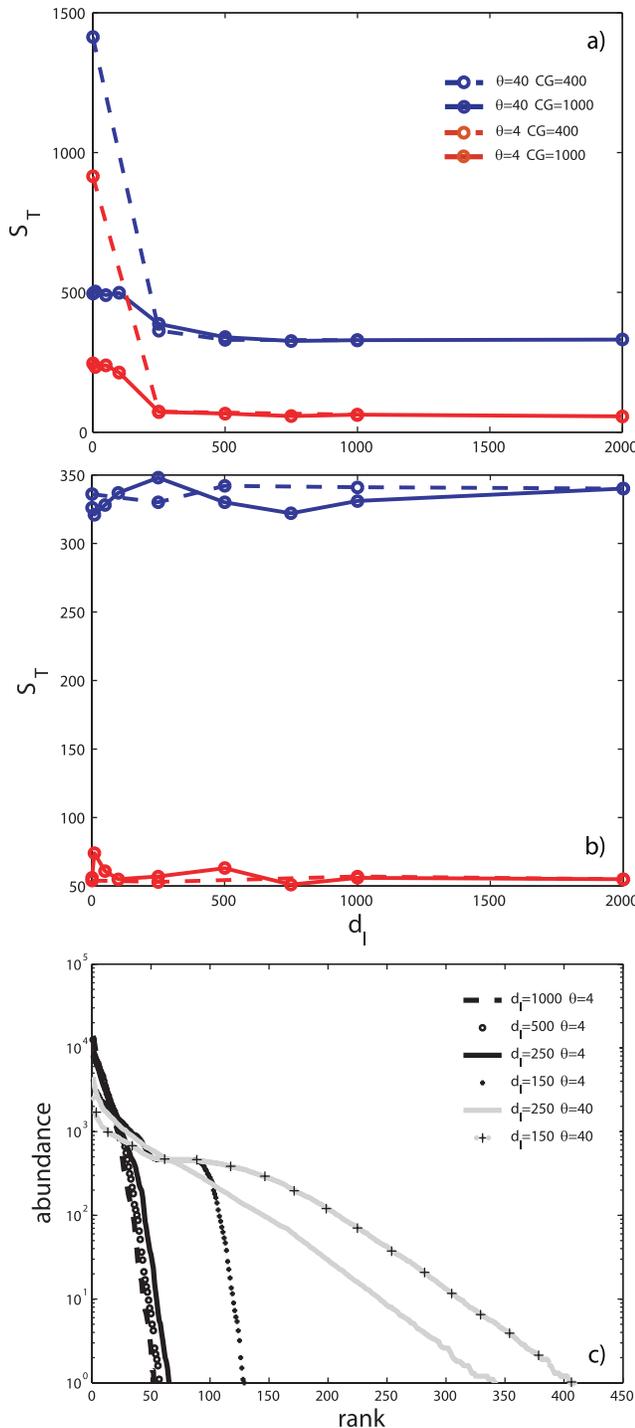


Figure 5. Rank-abundance curves associated with (left) the exponential and (right) the exponential-Cauchy kernel dispersal for (a and b) the OCN, (c and d) the Cordevole basin, and (e and f) the Tanaro basin. The resolution invariance of the RA curves is observed for both sets of parameters used in the simulations (Table 2). $S_{\mathcal{F}}$, that is, the maximum rank, is very invariant (~ 300) regardless of the basin, the resolution, and the dispersal mechanism because the latter is sufficiently nonlocal. This is because the total species richness depends critically on N and θ .

ment with *Chave et al.* [2002] and with the results shown in Figures 6a and 6b. The number of species at stationary state S_T is quite insensitive to river basin, resolution or ecological scenario. This is suggested to stem from the fact that the total species richness depends more critically on N and θ as long as the dispersal is sufficiently nonlocal. If the dispersal is extremely local, S_T tends to increase (Figure 6a).

[22] Figures 6a and 6b show the dependence of S_T on d_l and θ for the exponential and the exponential-Cauchy kernel cases, respectively, for the Tanaro basin. Two values of θ have been considered: $\theta = 4$ (red lines), and $\theta = 40$ (blue lines) for $CG = 400$ (dashed lines) and $CG = 1000$ (solid lines)



line). The resolution dependency of RA is marked by the gap between the $CG = 400$ and $CG = 1000$ resolution curves that shows a meaningful variation of S_T only for very small values of d_l .

[23] In the case of the exponential kernel (Figure 6a) there is a clear threshold value of the dispersal length, i.e., about $d_l = 250$, that determines the transition for the rank-abundance pattern to hold independently of the resolution and the diversification rate θ ($d_l > 250$). It is in this sense we refer to the resolution independency of the RA pattern. Below $d_l = 250$, the total number of species at stationarity state, S_T , results sensitive to the coarse-graining resolution; the RA pattern for $d_l < 250$ exhibit a plateau that means the presence of many common species with the same abundance. This happens because the dispersal length is so small that the movement of species is very limited: for $d_l = 1$, S_T tends to coincides with the number of local communities, n , in which on average there is only one species. In the case of the exponential-Cauchy kernel (Figure 6b) the resolution invariance is consistent for all values of the dispersal parameter and the resolution. The difference of S_T for $\theta = 4$ and 40 is similar to the exponential kernel dispersal case, but for very small d_l (owing to the fat tail character of the dispersal) the species are able to move along the whole network thus maintaining the resolution invariance of the RA pattern. Where in fact S_T tends to be equal to the number of local communities, a drop is produced in the rank-abundance curves (see Figure 6c) that results in changes in the maximum value of the rank between coarse-grained resolutions (the number of local communities n decreases as the CG resolution increases). In the case of global dispersal (i.e., a dispersal kernel $K_{ij} = 1/n$) the invariance of the rank-abundance plot is indeed observed.

[24] Figure 6c reports the rank-abundance pattern for nontrivial values of d_l and different θ at resolution $CG = 1000$ of the Tanaro basin, so $d_l = 1000$ in this case is equal to the mean distance between two neighboring communities. Increasing the diversification rate, e.g., for $\theta = 40$ (solid and black crosses and grey lines, Figure 6c), the increase in the number of species is much stronger than when assuming lower values of the dispersal parameter (solid and dotted black lines) at the same CG resolution. Thus for higher values of θ the number of species at stationary state, S_T , is

Figure 6. (a and b) Dependence of d_l and θ on the total number of species at stationary state, S_T , for the exponential and exponential-Cauchy kernel cases, respectively, for the Tanaro basin. Two values of θ have been considered as an example: 4 (red lines) and 40 (blue lines) for $CG = 400$ (dashed lines) and $CG = 1000$ (solid line). The resolution dependency of RA is marked by the gap between the $CG = 400$ and $CG = 1000$ resolution curves that shows a meaningful variation of S_T for very small values of d_l . (c) Rank-abundance curves for the Tanaro basin in the exponential dispersal for the resolution $CG = 1000$, $\theta = 4, 40$, and different values of the dispersal length $d_l = 150, 250, 500, 1000$ with different line styles according to the legend. For the Cordevole and the OCN the results are analogous to these shown for the Tanaro. Table 2 reports the values of the parameters for the simulated ecological scenarios a and b.

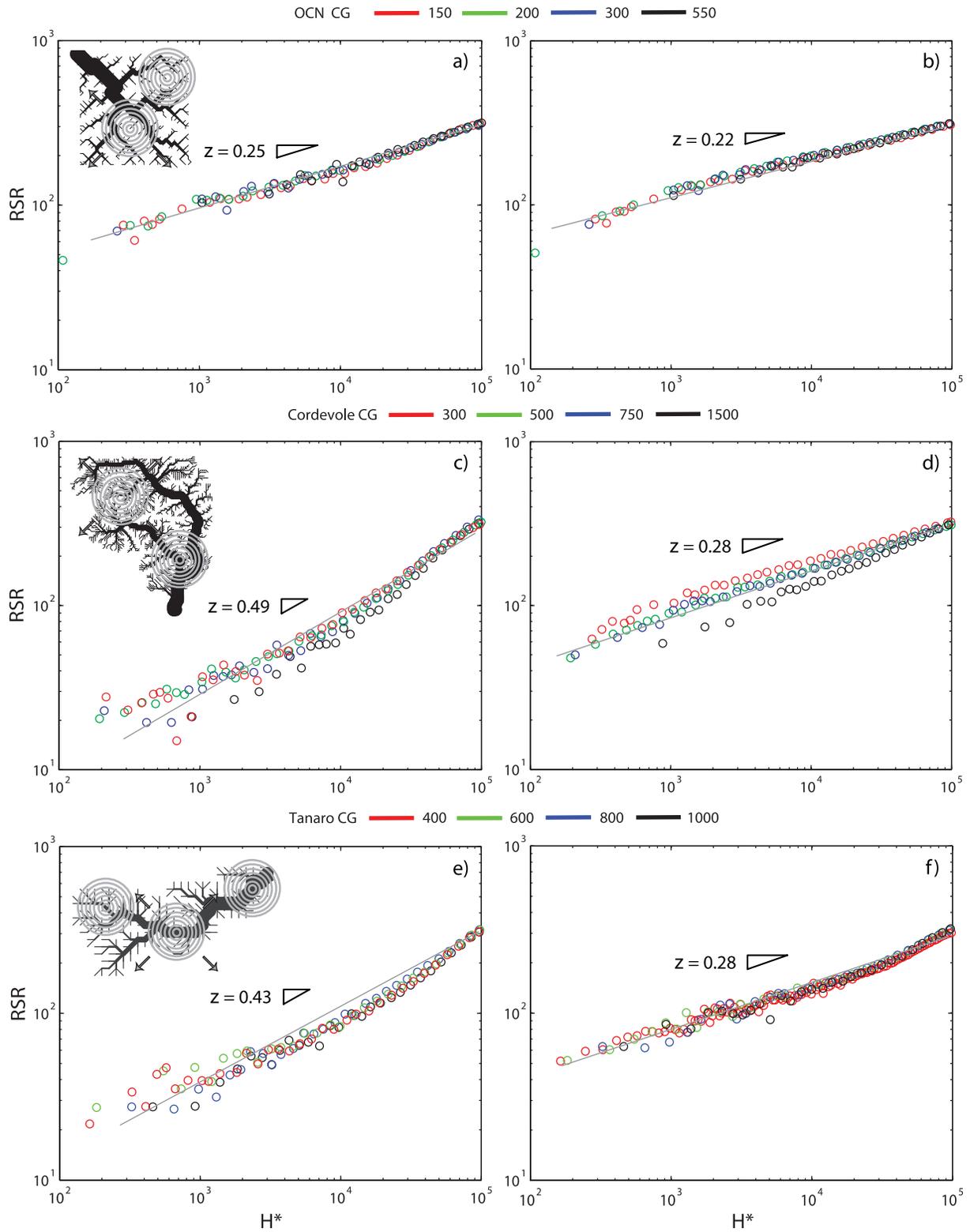


Figure 7. SAR derived between $RSR = \langle S \rangle$ versus H^* for (a and b) the OCN and (c and d) the Cordevole and (e and f) Tanaro basins at different resolutions for two types of dispersal kernel, namely, (left) exponential and (right) exponential-Cauchy kernels; the circles represent the binning averages. The insets illustrate the approach for computing the species richness at regional scale. The estimated exponents are derived by linear and jackknife regressions [Warton *et al.*, 2006], and the coefficient of determination, R^2 , is calculated (Table 2).

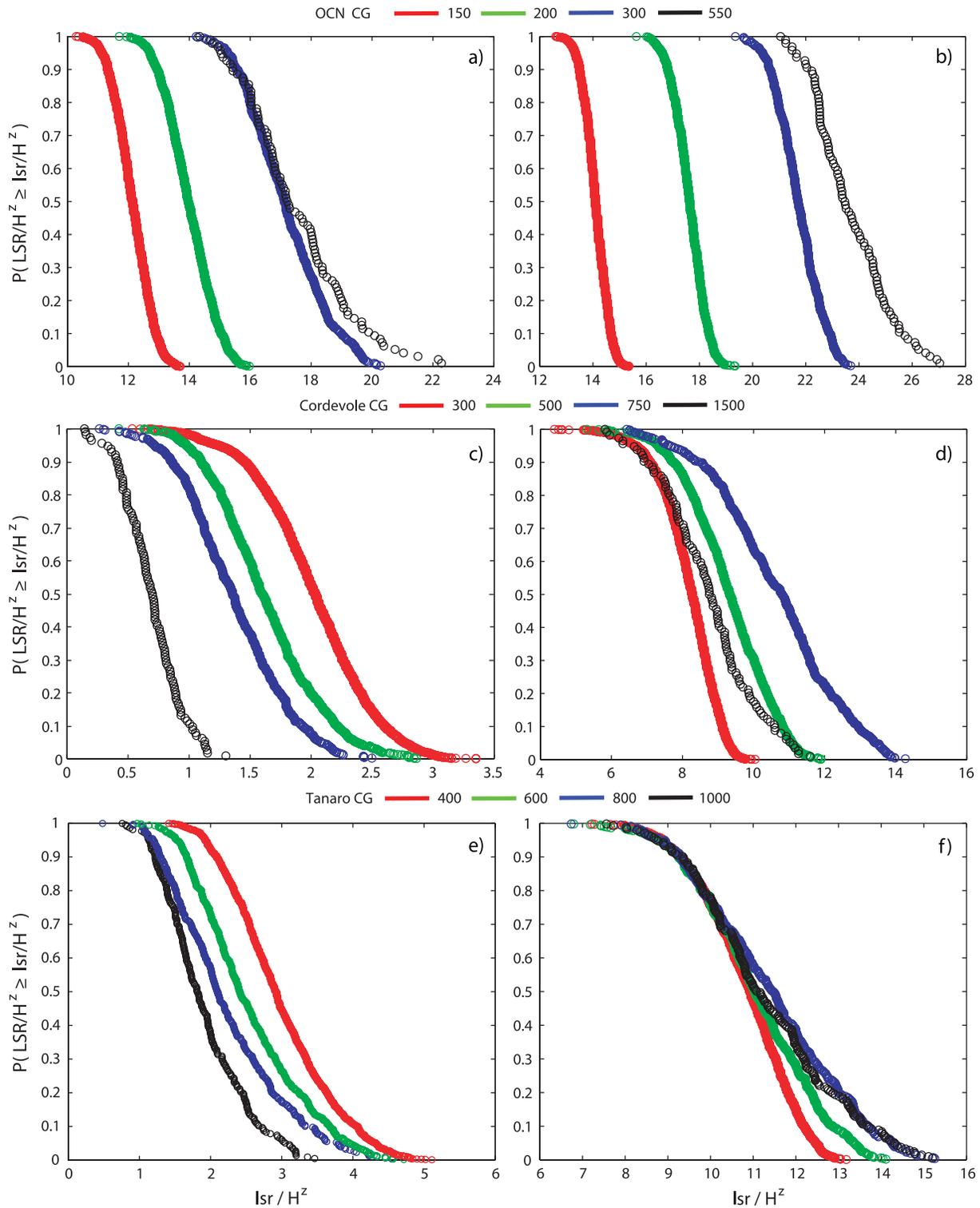


Figure 8. Rescaled probability of exceedance of local species richness, $P(LSR/H^z \geq lsr/H^z)$, at different resolutions for the (left) exponential and (right) exponential-Cauchy kernel for the (a and b) OCN and (c and d) Cordevole and (e and f) Tanaro basins. The distributions do not collapse onto the same curve and do not exhibit a power law behavior. The exponents z are those derived by fitting the species-area relationship in Figure 7.

larger. For intermediate values of d_l and θ , the RA patterns are not affected by the resolution. We also note that the effect of coarse-graining (CG) is intrinsically present for the discretization of the dispersal kernel structure, K_{ij} versus L ;

this is particularly evident when d_l is small and the CG resolution is coarse. For the Cordevole and the OCN the results shown in are analogous to these shown for the Tanaro in Figure 6.

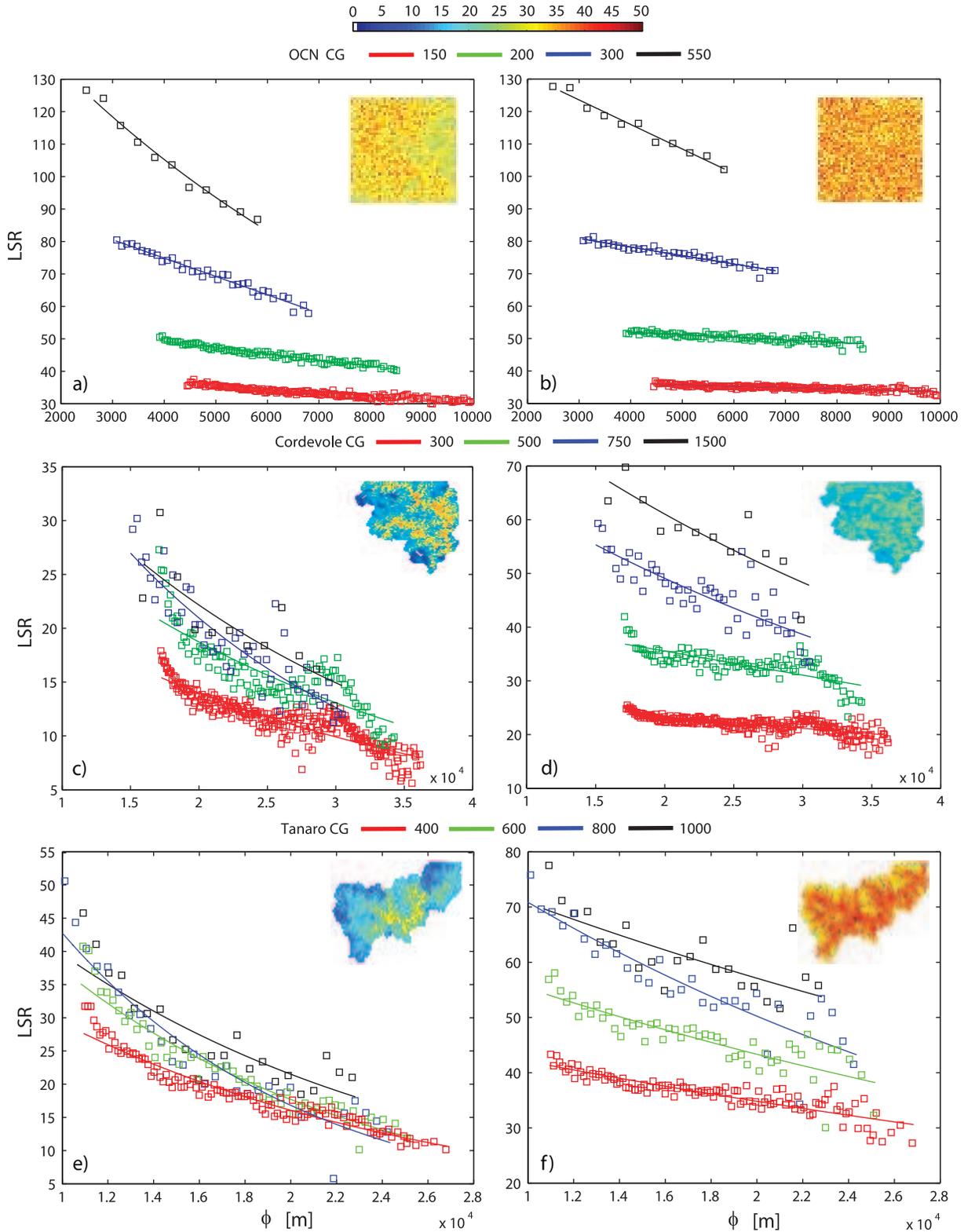


Figure 9. LSR versus the diameter ϕ at different resolutions for the (left) exponential and (right) exponential-Cauchy kernel for the (a and b) OCN and (c and d) Cordevole and (e and f) Tanaro basins. The top legend specifies the color for each resolution, and the color bar refers to the insets in each plot showing the LSR pattern related to each ecological case.

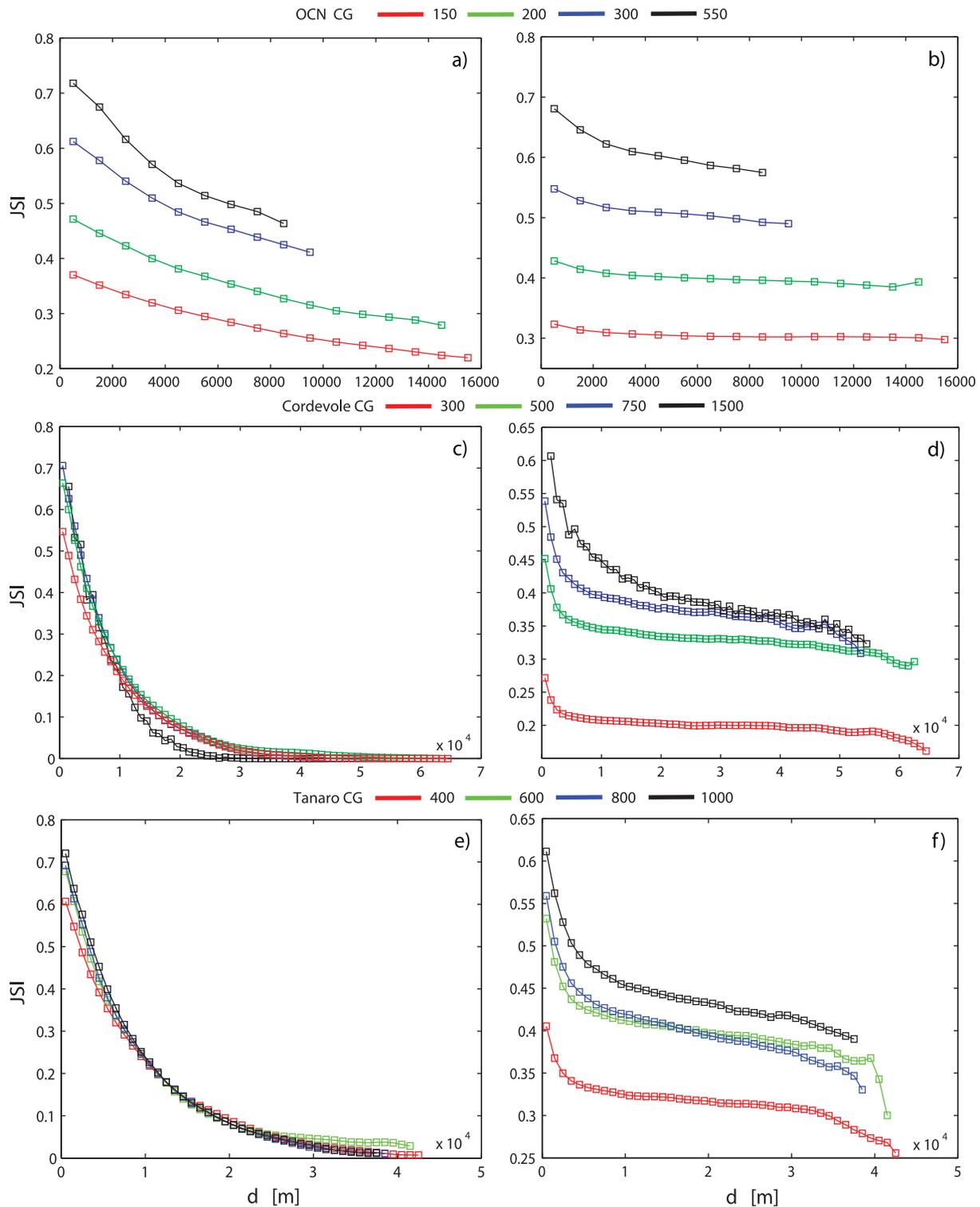


Figure 10. Plots of the average JSI versus d at different coarse-graining resolutions for the (left) exponential and (right) exponential-Cauchy kernel for the (a and b) OCN and (c and d) Cordevole and (e and f) Tanaro basins.

[25] Figure 7 illustrates the dependence of the regional species richness RSR on area at various CG scales of aggregation. RSR is computed as the number of species S found over circular areas with different radii placed randomly over the basin. The RSR values are then binned depending on the habitat capacity H^* (i.e., the number of

sites) encompassed by the circular area and the average value is taken as representative of the ensemble. A species-area relationship (SAR) is expressed as $RSR \sim (H^*)^z$. Figures 7a, 7c, and 7e show $RSR = \langle S \rangle$ as function of H^* for ecological scenario a, and Figures 7b, 7d, and 7f show RSR for scenario b (Table 2). We note that for both types of

Table 3. Values of the Exponent z From the Species-Area Relationship $RSR \sim (H^*)^z$ in Ecological Scenarios a and b and for the Three Basins Considered^a

	OCN	Cordevole	Tanaro
Scenario a			
z	0.25	0.49	0.43
R^2	0.98	0.86	0.87
Scenario b			
z	0.22	0.28	0.28
R^2	0.99	0.87	0.98
τ	1.43 ± 0.01	1.44 ± 0.01	1.43 ± 0.02

^aValues are computed by taking the average number of species in circular areas with different radii randomly placed all over the basin. The slope z is derived by the linear and jackknife model [Warton *et al.*, 2006], and the coefficient of determination, R^2 , is reported. Here τ is the scaling exponent of $P(A \geq a)$, where A is the drainage area, and its variability is the standard error found by reducing major axis regression bootstrapping over cases and resolutions [Warton *et al.*, 2006].

kernels the different levels of coarse graining exhibit a collapse of RSR versus H^* . The species-area relationship $RSR \sim (H^*)^z$ computed independently of the network structure, holds reasonably well for the case of dispersal with an exponential kernel and remarkably well when the dispersal includes a fat tail component for all the three basins. The values of the exponent z are estimated for all cases and networks and are given in Table 3. The slopes are computed using the linear and jackknife regressions [Warton *et al.*, 2006] and the coefficient of determination is derived. It is interesting to notice that the value of z estimated in the case of the exponential kernel dispersal for the Tanaro and Cordevole river basins, is considerably higher than those usually found in biogeographical species-area relationships for ecosystems in typical 2-D landscapes [MacArthur and Wilson, 2001]. This is not the case when the dispersal includes a fat tail component where the obtained values of z are in the range of those commonly observed. This suggests that species would adopt a fat tail dispersal strategy should they maximize their colonization and survivability [Davies *et al.*, 2004; Pearson and Dawson, 2004; Bohrer *et al.*, 2005; Soons and Ozinga, 2005; Nathan, 2006]. This is consistent with the invariance of S_T versus d_l in case b rather than in case a. This can indicate that the long-distance dispersal tends to diminish the impact of the network structure on the species-area relationship, and it is evidenced also by the more straight-convex character of the SAR (left plots versus right plots in Figure 7). Figures 7c and 7e show a double trend not present in Figures 7d and 7f. As suggested by Hubbell [2001], the SAR is constrained by the geometry of the biogeographic area in which the processes of origination, dispersal and extinction act. The upturn of the SAR occurs in correspondence to a correlation length, independent of θ , that represents the spatial scale of the geometric constraint imposed by the landscape [Hubbell, 2001]. We do not observe a significant difference in the value of z in the two different dispersal cases for OCNs (Figures 7a and 7b) perhaps because of the shape of the basin.

[26] We further investigate the effects of coarse graining on the local species richness, LSR, defined as the number of species present in each local community at stationarity. LSR represents a measure of local biodiversity. Figure 8 shows the probability of exceedance of the normalized local species richness, LSR/H^* , for the OCN (Figures 8a and

8b), Cordevole (Figures 8c and 8d), and Tanaro river basin (Figures 8e and 8f) where H is the habitat capacity of each local community and z is the exponent of the species-area relationship (see Figure 7). The probability $P(LSR/H^* \geq lsr/H^*)$, however, does not collapse onto a unique curve. In the exponential-Cauchy dispersal scenario (right plots) the overlapping of the curves is more evident than in the exponential dispersal scenario (left plots), as observed for the species-area relationship (Figure 7), because of the higher homogeneity of the LSR in the latter case. This is more evident for the two real river basins, Cordevole and Tanaro, particularly for the latter probably because of its more pronounced elongation. Higher values of LSR are observed in the exponential-Cauchy kernel dispersal than in the exponential kernel dispersal.

[27] Figure 9 shows the behavior of the LSR as function of the diameter ϕ for the OCN (Figures 9a and 9b), Cordevole (Figures 9c and 9d), and Tanaro river basin (Figures 8e and 8f), in the exponential dispersal case (left plot) and exponential-fat tail dispersal case (right plots). The LSR generally increases from the finest to the coarsest resolution (because of the decrease in the number of links n while the total number of individuals N remains constant) and ordinarily decreases when the diameter ϕ becomes larger. High values of the LSR are expected for stream links with small diameters because they are well connected to all the other links in the basin and thus, on the average, species can travel to links with small diameters more frequently than to their large-diameter counterparts. This is particularly true in the case of exponential kernels because, if the spreading of species shows a fat tail component, they can move over long distances resulting in more regular patterns. This is suggested by Figure 9 where the values of the LSR are quite uniform in the three basins for the ecological scenario b. Large LSR exists at the outlet, along the mainstreams of the network, and in source areas it is quite big. Note that high values of LSR across all coarse-graining resolutions exist in links where the diameter, ϕ , is small. From the LSR pattern the structure of the network emerges in the case of the exponential dispersal kernel, Figures 9a, 9c, and 9e, and the gradient of species richness along the mainstream toward the source areas of the basin is relatively sharp. For the case of the exponential-Cauchy dispersal kernel, Figures 9b, 9d, and 9f, the LSR pattern is relatively homogeneous and the along-stream gradient in species richness is not as steep as in case a. The insets of the plots are the LSR patterns properly color coded (top of Figure 9). We find that the average value of LSR in the whole basin decreases with the diameter for every resolution. The OCN shows the largest values of the maximum and mean LSR regardless of resolution; the mean and maximum values of LSR are larger for the Tanaro than for the Cordevole owing to the larger diameter. It is not observed a relevant difference in the LSR versus ϕ pattern between the two dispersal cases for the OCN (Figures 9a and 9b).

[28] As a descriptor of the spatial structure of biodiversity, β -diversity, we use the Jaccard similarity index, JSI, defined as

$$JSI_{ij} = \frac{LSR_{ij}}{(LSR_i + LSR_j - LSR_{ij})}, \quad (3)$$

where LSR_{ij} is the number of species that are common to both links i and j , and LSR_i is the total number of species in link i . We examined the JSI index as a function of the along-stream distance, d , between links. It ranges from 0 if two local communities share no species, to 1, if their species composition are identical. Figure 10 reports the decay with distance of the JSI index for the OCN (Figures 10a and 10b), Cordevole (Figures 10c and 10d), and Tanaro river basin (Figures 10e and 10f), in the exponential dispersal case (left plots) and exponential–fat tail dispersal case (right plots). As expected, the pairwise similarity of species among links at a given distance d is greater for the ecological scenario b where the Cauchy component of the dispersal kernel plays an important role. In Figures 10c and 10e for Cordevole and Tanaro, respectively, JSI values in case a for all resolutions basically coincides. The decay of JSI is faster in the case of exponential kernel a implying that local communities at large distances tend to have very different species composition. In all cases the value of JSI = 1 for $d = 0$ is not included. For the OCN there is a relevant difference for the pairwise similarity pattern between resolutions even in the exponential dispersal case, but the decay of JSI versus d is faster than in case b. This behavior could be related to the limited extension and the shape of the OCN employed. We finally note that simulations with different values of the total number of individuals, N , and speciation rates, θ , do not produce significant differences in the computed biodiversity patterns and the above remarks.

5. Conclusions

[29] The following conclusions are worth mentioning.

[30] 1. By employing a metacommunity model for species that act neutrally, the study of the macroecological descriptors (species richness at local and regional scale, and the pairwise species similarity) in river basins has shown the validity across resolutions of a species-area relationship dependent on the different network structures and the diverse ecological scenarios. In the case characterized by a kernel whose structure is the combination of an exponential at short distances, and a fat tail that controls the dispersal at large distances, the exponent of the species-area (SAR) relationship assumes quite different values from the case with only the exponential but they match those found in real landscape. For both the exponential dispersal and the exponential–Cauchy dispersal kernels a unique regime appears for the SAR.

[31] 2. The results suggest that the local species richness (LSR) and the species' similarity index (JSI) depend on the coarse-graining resolution used in the analysis. Thus, the robust invariance of the geomorphological characters of river basins does not imply universality in the resulting ecological patterns seen at different resolutions under the hypothesis of neutral dynamics. However, future work should be focused on possible scaling relations of these ecological indicators, not only in function of the resolution but also in function of the scale of analysis.

[32] 3. The rank-abundance curves shows a resolution-invariant character regardless the specific value of the diversification rate and for a broad range of dispersal lengths. In the exponential dispersal case there exists a limited region for $d_l < 250$ in which the total number of species varies significantly with the resolution and the RA

pattern have many common species with the same abundance. In the exponential–Cauchy dispersal case the invariance of RA patterns is granted for all values of the dispersal length. Moreover the number of species at stationary state S_T is quite insensitive to different river basins and ecological scenarios.

[33] Thus we may reinforce earlier suggestions about the importance of the network structure on biodiversity patterns.

Notation

Geomorphological parameters

- A Drainage area (pixels).
- ϕ Geomorphological diameter (m).
- d Geomorphological distance between links (m).
- n Total number of links in the space-filling network.
- δ Pixel side length at the finest CG resolution (= 100 m).
- λ Coarse-graining resolution parameter.

Ecological parameters

- N Total number of individuals in the basin, or habitat size (= 1×10^5).
- S_T Total number of species in the basin at stationary state.
- S Average number of species encompassed in a circular area of radius r at a link.
- H Link habitat capacity ($\simeq N/n$).
- H^* Number of individuals encompassed in a circular area of radius r at a link.
- d_l Dispersal length parameter (m).
- θ Diversification rate (number of new species introduced at each time step = $N\nu$).
- ν Per site diversification rate (θ/N).
- b Cauchy-kernel parameter.
- K_{ij} Fraction of individuals produced in j that go into i .
- LSR Local species richness (number of species at link i).
- JSI Jaccard similarity index.
- RSR Regional species richness ($=\langle S \rangle$).

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