unpaired t-test, $t = 4.456$, $P = 0.002$, and between five groups 'with' and four groups 'without announcement' after the block treatment, d.f. = 7, unpaired t-test, $t = 6.631$, $P = 0.0003$). Thus, the pending risk of further rounds of indirect reciprocity prevented cooperation in the public goods game from declining at least over four consecutive rounds.

Obviously, refusing to give in the public goods game reduced the reputation of a player to a similar extent as if this person had refused to give in the indirect reciprocity game: his potential donor in the next round of indirect reciprocity just followed the rules for indirect reciprocity and refused to give to someone with a low image score. This is different from punishing because it does not need any special punishing rule or motivation, and the potential donor actually saves money by refusing to give. A recent theoretical analysis[21] suggests that reputation is essential for fostering social behaviour among selfish agents, which is confirmed experimentally here. The inclusion of reputation effects in the corresponding dynamical models leads to the evolution of economically productive behaviour, with agents contributing to the public good and either punishing those who do not or rewarding those who do[21]. Providing help in the indirect reciprocity game is a form of reward.

Cooperation in the public goods game paid off. Groups that alternated rounds of indirect reciprocity and public goods games, and thus were more cooperative in the public goods game, earned significantly more money during the first eight rounds of the public goods game than did groups that played the two games in blocks of eight rounds each (Fig. 2b). This shows that the 'tragedy of the commons' was no longer a tragedy; instead, the commons became productive and could be harvested. Two people usually interact in more than one situation, therefore their actions in one context may influence actions in another[22]. Many social dilemmas are a type of public goods game[6], others have been identified as a type of indirect reciprocity game[4]. It therefore seems likely that the kind of interaction that we have staged experimentally occurs naturally in our society. There might be hidden social dilemmas that would show up only if the interaction with another game were removed. □

Methods

Indirect reciprocity game

Players were anonymous; each subject was assigned a pseudoname by the computer for the whole session of 20 rounds so that at any time, players could make their decisions contingent on the history of the game up to that time; each player knew his/her name but did not know who had been assigned the other names; the subjects were separated by opaque partitions and communicated their decisions with silent (piezo) switches; they knew that they would obtain their money after the game in a way that did not disclose their anonymity.

For the 'indirect reciprocity game'[20], each person was assigned repeatedly as either a potential donor or a potential receiver. For example, a potential donor, say 'Telesto', was asked on the public screen whether he would give to 'Galatea'. Telesto would loose DM 2.50 from his account and Galatea would gain DM 4 on her account if Telesto decided 'yes'. Telesto's decision (yes or no) was displayed for 2 s on the public screen. Everybody knew about the contributions of all players, for example, whether Galatea had given in previous rounds when he/she had been playing as the potential donor. The subjects also knew that there would be no direct reciprocity; if A was the potential donor of B, B would never be the potential donor of A. In each round of the indirect reciprocity game, each of the six players was once a potential donor and once a potential receiver.

Public goods game

For the 'public goods game'[4], all six players were asked simultaneously whether they would contribute DM 2.50 to the public pool, the contents of which would then be doubled and redistributed evenly among all players irrespective of whether they had contributed. After all players had decided, each player's decision (yes or no), his/her contribution (that is, DM 2.50 or 0), and his/her gain (for example, DM 4.17 if all but one had contributed), was displayed below the pseudonames for 20 s.

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Species diversity enhances ecosystem functioning through interspecific facilitation

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Facilitation between species is thought to be a key mechanism by which biodiversity affects the rates of resource use that govern the efficiency and productivity of ecosystems[1–4]; however, there is no direct empirical evidence to support this hypothesis. Here we show that increasing the species diversity of a functional group of aquatic organisms induces facilitative interactions, leading to non-additive changes in resource consumption. We increased the richness and evenness of suspension-feeding caddisfly larvae (Insecta, Trichoptera) in stream mesocosms and found that the increased topographical complexity of the benthic habitat alters patterns of near-bed flow such that the feeding success of individuals is enhanced. Species diversity reduces 'current shading' (that is, the deceleration of flow from upstream to downstream neighbours), allowing diverse assemblages to capture a greater fraction of suspended resources than is caught by any species monoculture. The fundamental nature of this form of hydrodynamic facilitation suggests that it is broadly applicable to freshwater and marine habitats; in addition, it has several analogues in terrestrial ecosystems where fluxes of energy and matter can be

influenced by biophysical complexity[3,5,6]. **Thus, changes in species diversity may alter the probability of positive species interactions, resulting in disproportionately large changes in the functioning of ecosystems.**

Rapid rates of species extinction and homogenization of the world's biota provide compelling reasons for determining how changes in biodiversity might affect the functioning of ecosystems[7–9]. Current ecological theory predicts that species diversity can influence the consumption of resources that govern ecosystem processes through two types of effects: a 'complementarity effect', which occurs through either resource partitioning or facilitative interactions between species[2,10,11]; and a 'selection effect', which occurs whenever species diversity is correlated with the chance of resource use being dominated by a single, productive taxon[12,13].

To date, research has focused primarily on how selection effects and complementarity through resource partitioning influence the functioning of terrestrial assemblages of plants[8]. But evidence showing that positive species interactions are pervasive in nature has led to speculation that interspecific facilitation may be a key mechanism by which biodiversity enhances the performance of ecosystems[2,3,14]. Although research has shown that facilitative interactions between species of different functional groups can influence ecological processes[11,15,16], currently there is no mechanistic evidence that links species diversity in a functional group to positive species interactions that affect resource capture.

We studied a group of suspension feeders that are common in streams throughout the world (Trichoptera, Hydropsychidae).

Larval hydropsychid caddisflies construct silk catchnets in the pore spaces of a streambed and passively filter suspended particulate matter (SPM) from the water. We focused on a system of three species that occur together throughout the eastern United States (*Hydropsyche depravata*, *Ceratopsyche bronta* and *Cheumatopsyche* sp.). This simple system allows the identification and generalization of mechanisms, but still represents local levels of diversity that are common for this and other aquatic functional groups[17].

In aquatic habitats, biogenic structures are known to generate topographical 'roughness' (that is, spatial variation in surface features), which influences patterns of near-bed water flow and food delivery[18]. Because the physiognomy of feeding structures varies between species, we thought that increased diversity of hydropsychid caddisflies would increase bed roughness in a manner that alters near-bed flow and enhances the capture of organic resources. To test this hypothesis, we established two treatments of species diversity in stream mesocosms: 'single-species' streams (three streams, one per taxa) were colonized with 18 larvae of each caddisfly species; and 'mixed assemblages' (three streams) were established with 6 larvae of each taxa. This design resulted in a simultaneous increase in species richness and species evenness—the two aspects of species diversity. After allowing animals time to construct catchnets, we measured resource consumption by individual larvae and related this to the variation in near-bed velocity and bed roughness.

In streams with a mixed assemblage of species the total consumption of SPM was 66% greater, on average, than in single-species streams (Mann–Whitney $U = 9.00$, $P = 0.05$), and exceeded the total consumption in all species monocultures (Fig. 1a). The
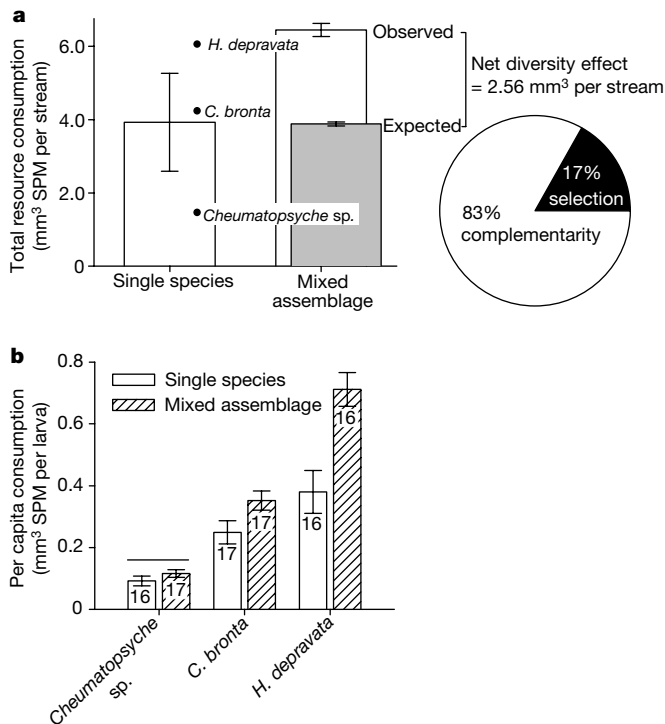

Figure 1 Effect of species diversity on resource consumption. **a**, Observed consumption of suspended particular matter (SPM) in single-species and mixed-assemblage streams (open bars) with expected values (shaded bar) calculated from species performances in monoculture (data points). Bars indicate the mean ± s.e. ($n = 3$ streams). Inset shows that the net diversity effect (observed minus expected resource consumption) was caused primarily by complementarity. **b**, Enhanced per capita consumption of taxa in mixed assemblages owing to interspecific facilitation. Bars indicate the mean ± s.e.; those not connected are significantly different ($P < 0.05$). Numbers are the final abundance of species in monoculture (open bars) or the summed number of larvae in the three mixed-assemblage streams (hatched bars).
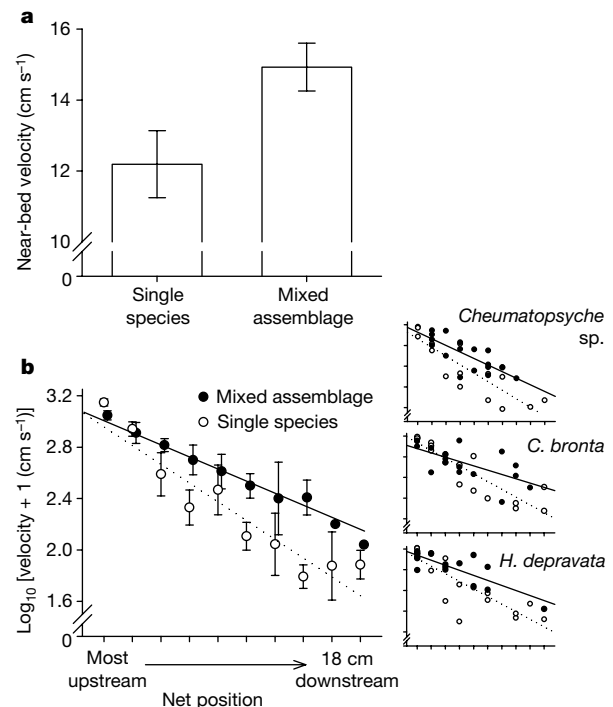

Figure 2 Effect of species diversity on flow. **a**, Near-bed current velocity measured at the entrance of caddisfly nets in single-species and mixed-assemblage streams (bars indicate the mean ± s.e. for 50 nets; means differ at $P = 0.02$). **b**, Upstream to downstream deceleration of flow into aggregations of suspension feeders. A significant interaction between treatment and net position (analysis of variance on log$_{10}$-transformed data, $F_{1,96} = 7.41$, $P = 0.01$) indicates that 'current shading' by upstream neighbours is more pronounced in single-species streams. Inset shows that there are consistent differences in current shading between diversity treatments for all taxa (axes are identical to those in main plot).

observed values of total SPM consumption in mixed assemblages was greater than that expected under the null hypothesis of no selection or complementarity effects[2] (paired $t = 11.41$, d.f. = 2, $P = 0.01$); thus, there was a significant positive net effect of species diversity on resource consumption (Fig. 1a). We partitioned the net diversity effect into two additive components due to selection or to complementarity[2]. We found that only 0.43 mm³ of the increase in SPM consumption above expected values (17% of the net diversity effect) was caused by selection (species-specific) effects. The remaining 2.13 mm³ (83%) was the result of species complementarity, which can result from either resource partitioning or interspecific facilitation of resource capture[2,4,14].

In a previous study of this experimental system[19], we showed that increasing the diversity of suspension feeders leads to an increase in the amount of SPM removed from stream water when the resource is not limiting, but diversity has no effect on SPM concentrations once the resource is depleted to limiting levels[19]. The latter result is contrary to what is expected from resource partitioning; that is, limiting resource concentrations should vary with species diversity when taxa differentially use a resource[10,19].

By contrast, the results of our current study are consistent with what is expected if suspension feeder diversity increases SPM consumption through interspecific facilitation of resource capture. We found that the feeding performance of individual larvae of each species was enhanced in the presence of other taxa. Per capita consumption of SPM by *H. depravata* and *C. bronta* increased by 87 and 41%, respectively, in mixed assemblages (*H. depravata*, $t = 3.76$, d.f. = 30, $P < 0.01$; *C. bronta*, $t = 2.13$, d.f. = 32, $P = 0.04$; Fig. 1b). Larval *Cheumatopsyche* also consumed 33% more SPM when inhabiting a mixed assemblage, but this increase was not significantly greater when compared with consumption by conspecifics in the single-species stream ($t = 1.20$, d.f. = 31, $P = 0.24$).

The hypothesis that increased resource consumption in mixed assemblages results from facilitative interactions is supported further by observed relationships between larval feeding performances and near-bed hydrodynamics. The delivery of food to suspension feeders is often proportional to flow velocity, particularly for passive filterers, such as hydropsychid caddisflies, that rely on water currents for the delivery of food particles[20]. We found that per capita consumption of SPM was positively correlated with near-bed velocity (measured within millimetres in front of the entrance to catchnets) for both the single-species ($r = 0.64$, $P < 0.01$, $n = 49$ larvae) and mixed-assemblage streams ($r = 0.50$, $P < 0.01$, $n = 50$ larvae). There were positive correlations between velocity and per capita consumption for each individual species in monoculture ($P < 0.01$ for all), and for *H. depravata* ($P = 0.02$) and *C. bronta* ($P < 0.01$) in mixed assemblages. These results indicate that increased resource capture in mixed assemblages resulted from alterations in near-bed flow. Indeed, we found that velocity measured at the entrance of caddisfly nets averaged 22% faster in mixed assemblages (Mann–Whitney $U = 1592$, $P = 0.02$; Fig. 2a).

Differences in mean near-bed velocity between treatments resulted from differences in the magnitude of 'current shading' (that is, the blocking of current from upstream to downstream neighbours, Fig. 2b). Whereas flow tended to decelerate from upstream to downstream neighbours in both systems, near-bed current in front of catchnets diminished by an average $-1.93 \mathrm{~cm~s}^{-1}$ per downstream net site when species were alone, as compared with $-1.47 \mathrm{~cm~s}^{-1}$ in mixed assemblages. This trend was consistent for all three taxa (Fig. 2b), and as a result the average larva in mixed assemblages experienced a current that was 2.73 cm s⁻¹ faster (22%) than when it was in monoculture.

Near-bed current velocity is known to be influenced by the density, height, spatial arrangement and topographical complexity of bed roughness elements[18,21–25]. Density, height and spatial arrangement of caddisfly nets did not contribute to differences in

current shading between the treatments. We standardized larval densities at the beginning of the experiment and found no difference between treatments at the end of the study ($t < 0.01$, d.f. = 4, $P = 1.00$). Although there was interspecific variation in net heights (mean was 6.54, 6.36 and 4.2 mm for *H. depravata*, *C. Bronta* and *Cheumatopsyche* sp., respectively), the mean height of nets for the three replicate single-species streams was equal to the mean height of nets in mixed assemblages ($t = 0.04$, d.f. = 4, $P = 0.97$). In addition, spatial aggregation of catchnets (the mean distance between neighbouring nets) was equivalent in the two treatments at the end of the experiment ($t = 1.44$, d.f. = 4, $P = 0.22$).

The only significant factor contributing to differences in bed roughness was topographical complexity (that is, the point-to-point variation in catchnet size measured as the standard deviation of net surface area). On average, topographical complexity was more than twofold greater in mixed assemblages than in single-species streams (s.d. = 18.61 versus 8.45 mm², respectively, $t = 6.41$, d.f. = 4, $P < 0.01$). Thus, placing taxa together led to streambeds characterized by non-uniformly sized elements of roughness. This is noteworthy because irregularly sized surface features can alter flow within an aggregation by inducing downstream eddies that increase diffusivity and turbulent mixing of water between the bed and overlying water column[21,23–25]. Our data indicate that altered patterns of near-bed flow in mixed assemblages may result from greater topographical complexity caused by variation in the morphology of suspension-feeding structures.

Our study shows that increasing the species diversity of a group of aquatic arthropods leads to interspecific facilitation, and thus diverse assemblages can outperform species monocultures. The form of facilitation that we describe—where individuals influence the delivery of resources to neighbours through biophysical interactions—is likely to be widespread in aquatic and terrestrial systems. Current shading is common in freshwater and marine environments[22,25–28], and similar phenomena occur in terrestrial plant canopies and soil communities in which individuals affect vertical and horizontal fluxes of resources (such as gases, water and nutrients) to neighbours[3,5,6]. The well known influence of structural complexity on fluid dynamics (both air and water)[18,23,29,30] suggests, however, that biophysical effects of diversity should modify resource shading, and therefore the rates of resource capture. It has been proposed[3], for example, that a positive relationship between bryophyte diversity and productivity results because a greater complexity of vertical structure helps to 'trap' water and facilitate plant survival during drought. Such differential impacts of species on the physical environment might be important mechanisms by which biodiversity generates positive interactions that enhance ecosystem functioning. □

Methods

Experimental design

The experiment was performed in recirculating stream mesocosms (0.1 m wide × 0.1 m deep × 1.0 m long) scaled to dimensions that maintain a dynamic similarity to conditions experienced by suspension feeders[19]. The working section of the streams (0.7 m downstream of the stream entrance) had 30 interstitial pores (3.6 mm deep × 15.0 mm long depressions such as found on rock surfaces) arranged in upstream to downstream rows. We released larvae uniformly over the surface of the working sections at the start of the experiment and allowed them to search freely for net sites. After 30 min of acclimation, the mid-channel flow was raised to 24 ± 1 cm s⁻¹ (mean ± s.d.). Larvae that drifted were captured and replaced with new individuals so that 18 animals initially colonized all streams. Larvae were given 7 d to construct catchnets, during which we added 46 mg of 63–149-μm suspended particulate matter per day to streams as food, set lighting to a 16:8 h day:night cycle, and maintained a constant water temperature (18–19 °C).

Near-bed flow

After 7 d, a Sontek 10-MHz acoustic doppler velocimeter (ADV) was used to record a 2-min time series (at 10 Hz, 1,200 readings) of three-dimensional velocity 5–6 mm above the streambed and 5–7 mm upstream of the entrance of every caddisfly net. To avoid acoustic interference, the sampling cell of the ADV was compressed to a nominal 4 mm in

height using software available from Sontek. From each time series we calculated mean near-bed velocity independent of flow direction. Mean near-bed velocity was compared between treatments using a non-parametric Mann–Whitney U-test because variances could not be transformed to satisfy parametric assumptions.

Resource consumption

After measuring near-bed flow, 278 mg of SPM stained with Rose Bengal dye was released as a single pulse into each stream[19]. Larvae were allowed to feed for 15 min (a duration less than gut passage times) before they were removed from their nets and frozen. We dissected larval guts later and measured the diameter and band length of stained SPM in foreguts using a dissecting microscope and ocular micrometer. Because foreguts are essentially cylindrical, the consumption of SPM by each larva was calculated as mm^3 SPM by $\pi \times$ band length in foregut $\times$ $(1/2$ foregut diameter$)^2$. Per capita consumption was compared between treatments using t-tests. Total resource consumption (the summed consumption of SPM by all larvae inhabiting a stream) was compared between treatments using a non-parametric Mann–Whitney U-test because variances could not be transformed to satisfy parametric assumptions. We used a paired t-test to compare observed resource consumption in mixed assemblages with the total expected SPM consumption[2].

Bed roughness

At the end of the experiment we recorded the downstream location of every caddisfly net and measured their maximum heights and widths. We calculated the average maximum height and density of the roughness elements, as well as their aggregation and topographical complexity. Aggregation measures the spacing between roughness elements as the mean euclidian distance between neighbouring nets. Topographical complexity measures the spatial uniformity or non-uniformity of roughness elements as the standard deviation of the parabolic area (in mm^2) of catchnets. An s.d. of 0 indicates a uniform streambed (no topographical complexity), whereas a higher s.d. indicates greater streambed complexity. We compared all four aspects of bed roughness between treatments using t-tests.

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Humans integrate visual and haptic information in a statistically optimal fashion

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When a person looks at an object while exploring it with their hand, vision and touch both provide information for estimating the properties of the object. Vision frequently dominates the integrated visual–haptic percept, for example when judging size, shape or position[1–3], but in some circumstances the percept is clearly affected by haptics[4–7]. Here we propose that a general principle, which minimizes variance in the final estimate, determines the degree to which vision or haptics dominates. This principle is realized by using maximum-likelihood estimation[8–15] to combine the inputs. To investigate cue combination quantitatively, we first measured the variances associated with visual and haptic estimation of height. We then used these measurements to construct a maximum-likelihood integrator. This model behaved very similarly to humans in a visual–haptic task. Thus, the nervous system seems to combine visual and haptic information in a fashion that is similar to a maximum-likelihood integrator. Visual dominance occurs when the variance associated with visual estimation is lower than that associated with haptic estimation.

The estimate of an environmental property by a sensory system can be represented by

$$\hat{S}_i = f_i(S) \qquad (1)$$

where S is the physical property being estimated and f is the operation by which the nervous system does the estimation. The subscripts refer to the modality (i could also refer to different cues within a modality). Each estimate, $\hat{S}_i$, is corrupted by noise. If the noises are independent and gaussian with variance σ_i^2, and the bayesian prior is uniform, then the maximum-likelihood estimate

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