wind because both variables can be simultaneously retrieved. Previous analyses of the TIWs and the cold tongue have shown a close coupling between SST and wind and have suggested that the coupling is due to marine boundary layer (MBL) dynamics rather than to pressure gradients (*23–25*). Over warm water, the MBL is unstable, air turbulence enhances the exchange of momentum from winds aloft to the surface, and higher surface winds result. For cold water, the boundary is stable, the vertical exchange of momentum is less, and the surface winds are lower. TMI SST and wind fields (Fig. 2) reveal how highly correlated SST-wind couplings are on a much finer temporal-spatial scale (measured weekly at a resolution of 50 km) than previously reported. The linear correlation between the weekly SST and the surface wind at a resolution of 50 km is 0.78, and the observed relation between SST and wind is consistent with a relatively simple boundary layer model (Fig. 3) (*26*).

Cold wakes from storms and hurricanes have been studied in the past by means of infrared SST observations (*10*, *27*, *28*), but the analysis has been encumbered by the extensive cloud cover associated with these storms. Figure 4 compares the TMI SST field with infrared SST imagery (*29*) of Hurricane Bonnie on 24 to 26 August 1998. The microwave imagery provides nearly complete coverage, whereas much of the infrared imagery is blocked by clouds. Figure 4 also illustrates another possible problem for the infrared retrievals. The Gulf Stream east of Cape Hatteras, which is clearly resolved in the microwave imagery, is barely visible in the infrared imagery. We attribute this to undetected clouds obscuring the ocean surface.

Storm track prediction has steadily improved along with better numerical models and observations, but the prediction of storm intensity falls short of expectations (*4*). Several studies (*4*, *30*) have shown that after initial development, the intensity of severe storms is strongly influenced by the thermodynamic structure of the upper ocean, and an accurate prediction of the storm's future intensity requires measurements of the ocean's thermal structure ahead of the storm. Extensive cloud cover around storms often prevents infrared satellite SST measurements. Microwave SST retrievals clearly have the potential to improve these important forecasts, as was shown in the 1998 hurricane season. In late August, Hurricane Danielle closely followed Hurricane Bonnie. Danielle's intensity dropped significantly as it passed over a region of cold water caused by Bonnie (Fig. 4A). Because of the cloud problem in infrared SST retrievals, the National Hurricane Center (NHC) uses a low-resolution SST field (measured weekly at a resolution of 100 km) (*8*) from the previous week (Fig. 4C) in their intensity models (*31*). For the Danielle prediction, this weekly SST product was missing Bonnie's cold wake, which may explain why most official forecasts overestimated Danielle's intensity by 30 to 40 knots (*32*).

TMI is the first in a series of satellite microwave radiometers that will measure SST under nearly all weather conditions. In the next 2 years, two Advanced Microwave Scanning Radiometers (AMSR) will be launched on U.S. and Japanese spacecraft. The AMSR will have an additional 6.9-GHz channel that will enhance SST retrieval. Later in the decade, the Conical Microwave Imager Sounder (CMIS) will be a primary sensor flying on the National Polar Orbiting Environmental Satellite System. CMIS, with its full complement of polarimetric channels, will be able to measure the global SST field to an accuracy of about 0.2°C at a spatial-temporal resolution of 50 km and 3 days.

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Cooperation Through Image Scoring in Humans

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The "tragedy of the commons," that is, the selfish exploitation of resources in the public domain, is a reason for many of our everyday social conflicts. However, humans are often more helpful to others than evolutionary theory would predict, unless indirect reciprocity takes place and is based on image scoring (which reflects the way an individual is viewed by a group), as recently shown by game theorists. We tested this idea under conditions that control for confounding factors. Donations were more frequent to receivers who had been generous to others in earlier interactions. This shows that image scoring promotes cooperative behavior in situations where direct reciprocity is unlikely.

Cooperative behavior in social dilemma situations (*1*) can sometimes be understood as reciprocal altruism (*2*). However, humans often help others even if the altruistic act is not likely to be returned by the recipient (*3*). Recent computer simulations and analytical models (*4–6*) have shown that this can be beneficial in the long run and can be an evolutionarily stable strategy. The idea is that helping someone, or refusing to do so, has an impact on an individual's image score within a group. This score reflects an individual's reputation and status, which are constantly assessed and reassessed by others and which may be taken into account by them in future social interactions. We tested this idea with 79 first-semester students who were naïve with respect to these recent theoretical developments. They were distributed among eight groups and asked to play a game in which they could repeatedly give money to others and receive from others, but they were told that they would never interact with the same person in the reciprocal role. As in the models (*4–6*), the cost of giving was smaller for the donor than was the benefit for the receiver (we donated the difference), whereas nongiving yielded neither costs nor benefits. The game was anonymous, but a player's history of giving or nongiving was displayed at each interaction. We found that donations were significantly more frequent to receivers who had been generous to others in earlier interactions. This is in accordance with theoretical models (*4–6*) and suggests that cooperation through indirect reciprocity takes place and is controlled by image scoring.

To ensure that every player was anonymous to us and to all of the others, the players each chose a plug to connect an opaque box with an impenetrable tangle of cables. They then chose a sitting place in a semicircle and placed their hand in the box in which they could secretly push one of two button keys that were now connected by the tangle of cables to numbered plugs handled by an operator. Figure 1 explains the procedure in detail.

Each player was provided with a starting account of 7.00 Swiss francs (SFr) (except in group 4, where each player started with an account of 13.00 SFr). The benefits of giving were always 4.00 SFr for the receiver, whereas the costs for the donors were 1.00 SFr (groups 1 through 3) or 2.00 SFr (groups 4 through 8). If the donors did not give, cost and benefits were 0.00 SFr for both. (For a standard of reference, a 100-g piece of Swiss chocolate costs around 1.50 SFr.) We played six rounds per group. Each player played once per round as "donor" and twice per two rounds as "receiver" in order to render the sequence of roles less orderly. Neither this nor any other information about the sequence was provided, nor was the end of the game announced.

For the analyses, we determined the image score of the players as described (*4*), i.e., giving increased it by 1 point and not giving decreased it by 1 point. The frequency of giving per group was relatively high [as expected (*4–6*), the range was 0.48 to 0.87]. As a consequence, the mean image score of the players increased from rounds 1 to 6 [repeated measures analysis of variance (ANOVA) on group means of receiver image scores was as follows: $F = 8.56$, degrees of freedom (df) = 5, $P = 0.004$], reaching group means of, on average, 1.69 (SE = 0.48) at the end of the game. The groups with a lower cost of giving or with a higher starting account (groups 1 through 4) donated more often ($t = 2.05$, $P = 0.05$) and achieved a higher mean image score at the end of the game ($t = 2.74$, $P = 0.02$) than the groups with high costs of giving and a low starting account.

The receivers' history of giving had a significant impact on the donors' decision: the image score of the receivers who were given money for their account was on average higher than the score of those who got nothing (Fig. 2). This effect of image score did not significantly change during the course of the game: In a repeated measures ANOVA on group means of receiver image score, with rounds (six rounds, i.e., six group means per type of donors' decision) and donors' decisions (two types of decisions, i.e., two group means per round) as the repeated trial factors, the interaction between the two trial factors was as follows: $F = 1.36$, df = 5, $p = 0.21$.

Other than the one player who never gave

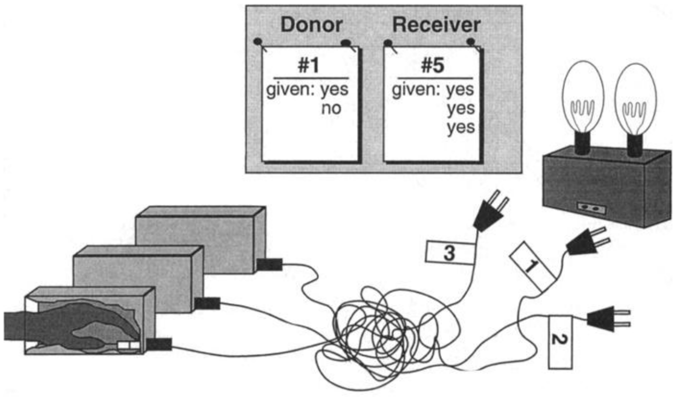

Fig. 1. To reveal a choice, all of the players had to push one of the button keys before the operator plugged one of the numbered plugs to a red and a green lamp (one of the lamps then lit up), and the players were allowed to release their button keys only after the operator had unplugged. To learn their own identification, each player drew a sheet with a sequence of four colors (red and/or green) from a pot, read it in secret, and indicated it with the procedure described above (the operator announced each identification number and plugged the respective plug four times in a row). Each time all players pressed their buttons. Afterward, a pair of players was randomly chosen, and the one who was chosen as "donor" was plugged to the lamps. She or he could either give something to the receiver (green light) or not (red light). The donor's choice was written down on a displayed protocol sheet so that everybody could see all of her or his previous choices in future interactions. Then, the next pair was chosen. After the game, each player could go alone into a room, open the envelope with her or his identification to take the money that she or he had earned during the game, and put the envelop back on the table in a way that did not reveal to the next individual whether it had been emptied or not.

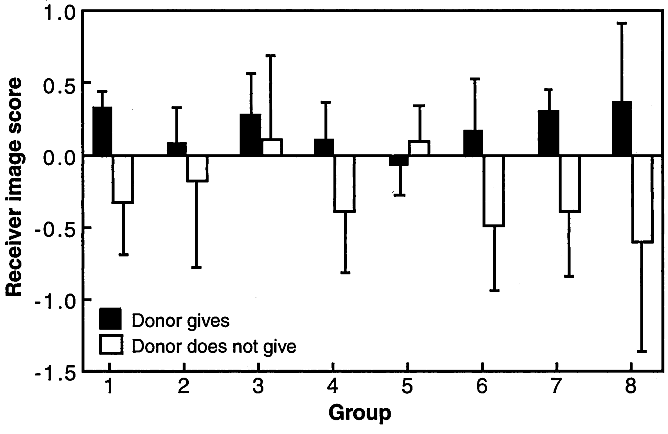

Fig. 2. The image score of the receivers if a donor gives something (solid bars) or does not give something (open bars). Data are shown as deviations from the means per group and round to correct for group and round effects (means ± SE, error bars). Repeated measures ANOVA with donors as replicates, with the mean (corrected) image score of the receivers if a donor gives or does not give as repeated measures, and with groups of players as grouping factor was as follows: df = 7; effect of group, $F = 0.11$, $P = 0.998$; giving or not giving, $F = 8.20$, $P = 0.006$; and interaction, $F = 0.64$, $P = 0.72$.

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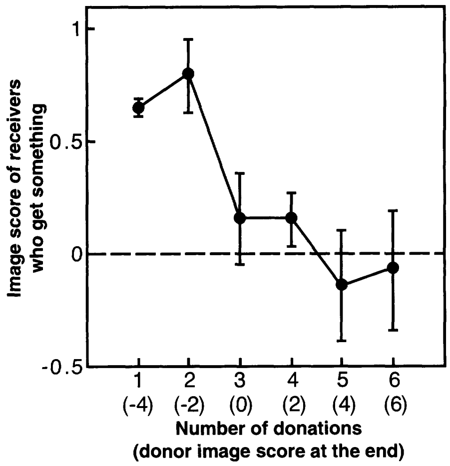

Fig. 3. Image score of receivers who obtained money on their account from donors who donated up to six times during the game (Kruskal-Wallis test, df = 5, $P = 0.04$, two-tailed). The figure shows the deviations from the means per group and round (averaged over all rounds) to correct for group and round effects (means ± SE, error bars).

anything (in group 6), those who donated rather rarely (less than three times, i.e., final image score of <0) showed a strong preference to give only to receivers with a relatively high image score (the mean deviations from group and round means were positive in 10 of 10 cases; $Z = 3.16$, $P < 0.01$), whereas with increasing generosity, the players appeared to be less discriminative with respect to the receiver's image score (Fig. 3). We did not find a significant correlation between the individuals' mean image score and their mean account per round (mean Spearman's r per group $= -0.19$; SE = 0.11; Wilcoxon test against 0: $n = 8$, $P > 0.05$, two-tailed).

Recent theoretical and experimental studies on cooperation games based on direct reciprocity support the idea that players learn from their opponents and adjust their strategy accordingly [e.g., (*7, 8*)]. Our results demonstrate that some form of image scoring is also used for indirect reciprocity (*3–6*) and hence may play a key role in the evolution of cooperation in larger groups (*9*).

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Species Diversity and Biological Invasions: Relating Local Process to Community Pattern

Jonathan M. Levine

In a California riparian system, the most diverse natural assemblages are the most invaded by exotic plants. A direct in situ manipulation of local diversity and a seed addition experiment showed that these patterns emerge despite the intrinsic negative effects of diversity on invasions. The results suggest that species loss at small scales may reduce invasion resistance. At community-wide scales, the overwhelming effects of ecological factors spatially covarying with diversity, such as propagule supply, make the most diverse communities most likely to be invaded.

Concern over the loss of species from ecological communities has stimulated renewed interest in the importance of species diversity to the functioning and stability of ecosystems (*1–4*). Of particular interest is the classic hypothesis that diversity enhances community resistance to biological invasions (*5, 6*). Support for this hypothesis has come from theoretical models (*7–10*) and experimental manipulations of diversity conducted in microcosms and other controlled environments (*11–16*). Although these studies have elegantly isolated the local or neighborhood effects of diversity on invasions, as well as the underlying mechanisms, the relevance and importance of these results for natural communities remain controversial (*17–19*). Factors other than diversity also influence invasions, yet most of the variation in these factors is eliminated in the relatively homogeneous experimental systems. By contrast, correlational studies of "uncontrolled" natural communities have most often shown that diverse assemblages are invaded more than their species-poor counterparts (*6, 19–23*). This result seems to contradict the models and experimental studies and has contributed to the impression that the relationship between diversity and invasibility defies generalization (*6, 17*). To address this apparent contradiction, and more generally to assess the importance of diversity to the invasion of a natural system, I performed a study coupling patterns of diversity and invasion with in situ manipulations of diversity in a natural context.

I conducted this study in the plant community bordering the South Fork Eel River in northern California. The system is dominated by *Carex nudata*, a tussock-forming sedge that provides the primary habitat for more than 60 plant species in the community. Each tussock is a discrete micro-island colonized by up to 20 perennial herbaceous plant and bryophyte species that depend on the tussock for stable substrate during winter flows (*24, 25*). The system is being invaded by Canada thistle (*Cirsium arvense*), common plantain (*Plantago major*), and creeping bent grass (*Agrostis stolonifera*), the propagules of which encounter numerous replicate tussocks containing varying numbers of native species.

In a survey of similarly sized tussocks over a 7-km stretch of river (*26*), the incidence of all three exotic plants was greater on more diverse tussocks (Fig. 1). Specifically, the presences of *Agrostis*, *Plantago*, and *Cirsium* were significantly (logistic regression $P = 0.001$, 0.008, and 0.004, respectively) and positively related to species richness (not including the invader). Although these correlations conflict with Elton's classic observation that species-rich systems are less invaded (*5*), they may not reflect the intrinsic effects of diversity. For example, positive correlations may result from a similar response of native and exotic species to environmental conditions (*6, 19–23*).

To test the effects of diversity on invasions in this system, I "invaded" tussocks in which the number of resident species was manipulated in situ. This approach left other factors that may influence invasibility free to vary (e.g., ambient nutrients and light, *Carex* stem number), but experimentally decoupled them from diversity. In late spring 1998, I removed all species from 65 randomly selected tussocks (each 350 cm^2) at a single large riffle (*27*). Each tussock was randomly assigned to one of five species rich-

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