

# Community rescue in experimental metacommunities

Etienne Low-Décarie<sup>a</sup>, Marcus Kolber<sup>b</sup>, Paige Homme<sup>b</sup>, Andrea Lofano<sup>b</sup>, Alex Dumbrell<sup>a</sup>, Andrew Gonzalez<sup>b</sup>, and Graham Bell<sup>b,1</sup>

<sup>a</sup>School of Biological Sciences, University of Essex, Colchester CO4 3SQ, United Kingdom; and <sup>b</sup>Department of Biology, McGill University, Montreal, QC, Canada H3A 1B1

Edited by Nils C. Stenseth, University of Oslo, Oslo, Norway, and approved October 2, 2015 (received for review July 7, 2015)

**The conditions that allow biodiversity to recover following severe environmental degradation are poorly understood. We studied community rescue, the recovery of a viable community through the evolutionary rescue of many populations within an evolving community, in metacommunities of soil microbes adapting to a herbicide. The metacommunities occupied a landscape of crossed spatial gradients of the herbicide (Dalapon) and a resource (glucose), whereas their constituent communities were either isolated or connected by dispersal. The spread of adapted communities across the landscape and the persistence of communities when that landscape was degraded were strongly promoted by dispersal, and the capacity to adapt to lethal stress was also related to community size and initial diversity. After abrupt and lethal stress, community rescue was most frequent in communities that had previously experienced sublethal levels of stress and had been connected by dispersal. Community rescue occurred through the evolutionary rescue of both initially common taxa, which remained common, and of initially rare taxa, which grew to dominate the evolved community. Community rescue may allow productivity and biodiversity to recover from severe environmental degradation.**

evolutionary rescue | migration | microbial diversity | toxicant | environmental degradation

**G**lobal environmental change is challenging the adaptive capacity of entire ecological communities. Communities exposed to severe anthropogenic stress may experience loss of biodiversity through species extirpation and large changes in ecosystem function. Populations of individual species may recover from stress via evolutionary rescue, if they possess sufficiently large and interconnected populations (1, 2) containing substantial genetic variation (3) and have experienced prior exposure to the stress (refs. 4 and 5; reviewed in ref. 6).

We extend the idea of evolutionary rescue to complex ecological communities, which may also survive initially lethal conditions and recover diversity through a combination of ecological and evolutionary processes. Community rescue occurs when a community comprising many species exhibits a rapid ecoevolutionary response to environmental stress that was lethal to the original community and all of its constituent populations (7), resulting in the recovery of a viable community. In this case the populations of many species will recover and some will increase from initial rarity. Communities can resist extirpation caused by the degradation of their environment or expand their range to degraded environments (8) through three kinds of processes. First, the harsh environment can trigger plastic changes eliciting the tolerance of some of the organisms via, for example, the activation or expression of physiological pathways. Second, the sorting of stress-tolerant species already present in the metacommunity can occur in the short term, in a fashion akin to the sorting of standing genetic variation in an asexual population by natural selection (9, 10). Third, when conditions are lethal to the original community and all of its constituent organisms, community rescue is required. Community rescue involves genetic change, including beneficial mutations, arising within populations in the longer term, leading to the evolutionary rescue of several or many initially susceptible species. Community rescue differs from community resistance [the maintenance of species composition when a community faces a disturbance (11)] and

community resilience [the return of communities to their original species composition after experiencing a disturbance (11)], because the degraded conditions were initially lethal to the whole community, so that community rescue, enabled by evolution, will result in a new community able to tolerate the degraded environment. The properties of the new community may differ from their original state and incorporate changes in species diversity, abundance, and interactions within the rescued community.

The processes that govern community rescue and mediate the frequency with which it occurs are poorly understood beyond simple models (7). Extending the conclusions reached from experiments with single species in metapopulations (1–5) to the rescue of diverse communities in a metacommunity, we expect community rescue following exposure to severe stress to be more frequent in diverse communities with high overall abundance that have previously experienced sublethal levels of the same stress. Prior exposure to sublethal levels of stress can occur through time when an environment is gradually degraded or through space when communities are dispersed across a heterogeneous landscape that contains conditions ranging from benign to those lethal to the initial community. Dispersal is expected to be a particularly important process governing the probability of community rescue. Preventing dispersal is known to hamper the survival of individual species and reduce the ecological and evolutionary resilience of communities (12, 13). Dispersal maintains local and regional diversity, allows gene flow, and enables species to shift their ranges to track habitable sites across the landscape through time (10). We designed an experiment to examine how the likelihood of community rescue is mediated by the interaction between environmental stress and dispersal within evolving metacommunities.

## Significance

**Global environmental change is challenging the adaptive capacity of entire ecological communities. Community rescue occurs when populations within a community evolve in response to an environmental stress that was initially lethal to all the constituent organisms. We studied how communities of soil microbes can extend the area they occupy to include conditions that were initially lethal, and how these communities can persist despite the degradation of environmental conditions. Our results suggest that entire communities have the potential to adapt to severe environmental stress. Community rescue is promoted by the initial diversity in the community, is more frequent among communities that have previously experienced intermediate sublethal levels of stress, and is facilitated by the dispersal of organisms across the landscape.**

Author contributions: E.L.-D., A.G., and G.B. designed research; M.K., P.H., and A.L. performed research; E.L.-D. and A.D. analyzed data; and E.L.-D., A.G., and G.B. wrote the paper.

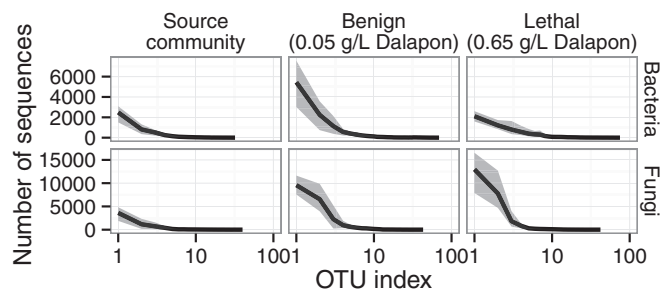
The authors declare no conflict of interest.

This article is a PNAS Direct Submission.

Data deposition: The sequence reported in this paper has been deposited in the European Nucleotide Archive (accession no. ERA445478). Data and analysis scripts are available in the Dryad database ([dx.doi.org/10.5061/dryad.65b2g](https://doi.org/10.5061/dryad.65b2g)).

<sup>1</sup>To whom correspondence should be addressed. Email: [graham.bell@mcgill.ca](mailto:graham.bell@mcgill.ca).

This article contains supporting information online at [www.pnas.org/lookup/suppl/doi:10.1073/pnas.1513125112/-DCSupplemental](http://www.pnas.org/lookup/suppl/doi:10.1073/pnas.1513125112/-DCSupplemental).



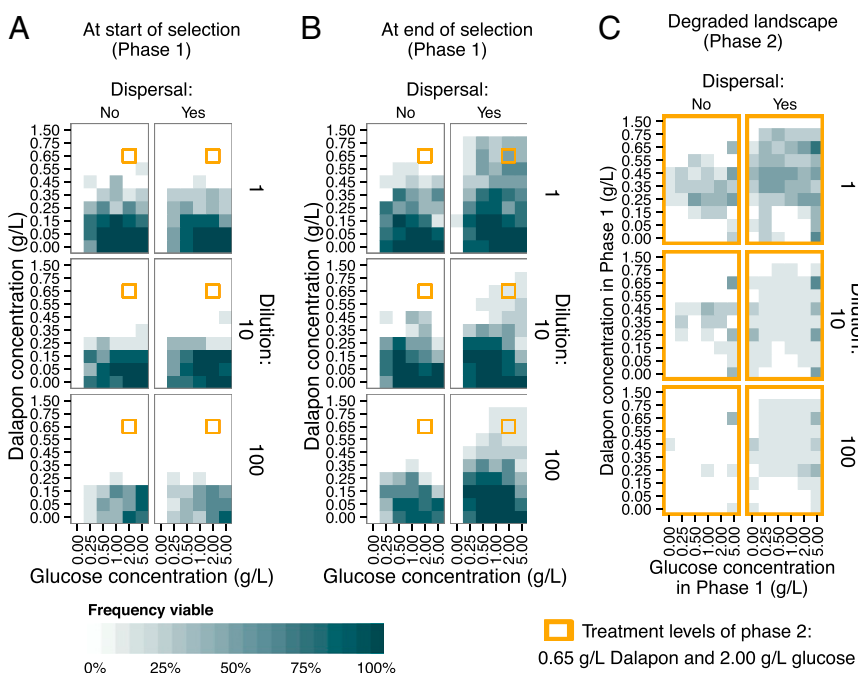
**Fig. 1.** Distribution of OTUs in source soil and in communities evolved on a polluted landscape. All source communities from soil and sediment samples yielded diverse communities of bacteria and fungi, but all were dominated by a few very common OTUs, with many rare types. Dilution would be expected to lead to the incremental loss of these rare types. Communities remain diverse even after selection and prolonged exposure to high levels of Dalapon (>42 OTUs for both bacteria and fungi). Shaded area represents the 95% bootstrapped confidence interval around the mean across the four source samples.

We used high-throughput methods to study community rescue in complex microbial communities responding to severe environmental stress caused by administering the herbicide Dalapon (2,2-dichloropropionic acid; background and justification for Dalapon use are provided in *Methods*). The source communities were soil and sediment samples from four sites in old-growth forest at Mont St-Hilaire, Québec, for which there is no history of exposure to any herbicide. The experiment proceeded in two phases. In phase 1, we evolved metacommunities on a heterogeneous landscape formed by a gradient of Dalapon pollution, increasing in concentration from zero to lethal, crossed with a gradient of glucose concentration, from zero to sufficient. In phase 2, we studied the response of these evolved communities to an abrupt degradation of their environment by transplanting adapted metacommunities to a uniform landscape in which Dalapon pollution levels were lethal to all source communities and all their constituent organisms. The composition of source and evolved communities was evaluated using amplicon sequencing.

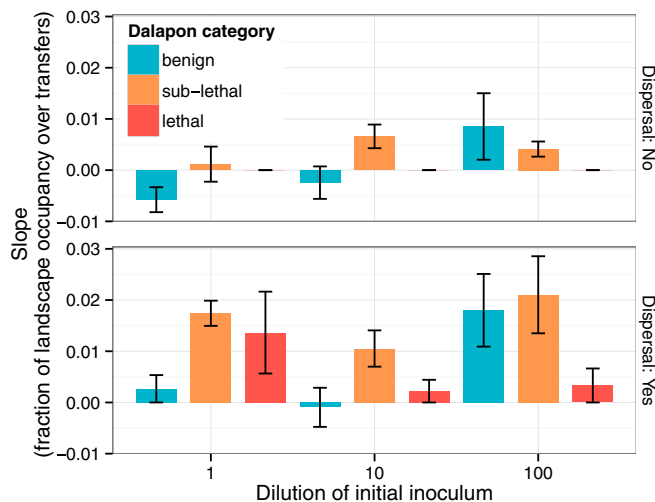
## Results

**Source Communities.** All source communities from soil and sediment samples yielded diverse communities of bacteria and fungi [mean (95% weighted bootstrap confidence interval) 61.8 (48.8–76.5) operational taxonomic units (OTUs) per source, representing 20.8 (17.0–25.5) identified genera]. As expected, the distribution was dominated by a few very common species, with a tail of many rare species (Fig. 1). This indicates that our dilution treatment ( $\log_{10}$  increments of dilution of source community) had a direct effect on richness in our experimental communities, by eliminating a portion of rare types.

**Phase 1.** Sites were categorized as benign, stressful, or lethal based on pilot data and the survival of the source communities at the beginning of Phase 1 (Fig. 2A). In benign sites (0–0.15 g/L Dalapon) the source communities grew in all wells that contained glucose. In sublethal sites (0.25–0.55 g/L Dalapon) the growth of the source communities was severely depressed, but at least one local community survived at each level of Dalapon. In lethal sites (0.65–1.50 g/L Dalapon), no growth could be initially detected. The amount of the landscape occupied at the end of phase 1 (Fig. 2B) and the rate at which the metacommunity expanded across the landscape during Phase 1 (Fig. 3) varied among these different categories of sites (Table S1; ANOVA,  $F_{2,60} = 5.495$ ,  $P = 0.006$ ). Benign sites were already almost fully occupied, except at high dilution, so the potential for further expansion was limited [mean 0.3% (–0.1 to 0.8%) increase in occupancy per transfer across all treatments]. The largest increase in occupancy was in sublethal conditions [mean 1.0% (0.7–1.5%) increase in occupancy per transfer across all treatments]. Expansion to sites that were lethal to the ancestral communities required both dispersal and the highest initial diversity [Fig. 3 and Table S1; mean 1.4% (0.1–2.6%) increase in occupancy per transfer with dispersal and the highest diversity in lethal conditions compared with mean 0.1% (0.0–0.3%) across all other treatments in lethal conditions, contributing to a significant interaction between dilution and Dalapon category, ANOVA,  $F_{2,60} = 6.112$ ,  $P = 0.004$ ]. Hence, the rate of expansion of the metacommunity into polluted zones of the landscape was promoted by dispersal among local communities and modulated by the degree of dilution of the source community (Table S1).



**Fig. 2.** Viable communities on experimental landscapes. Communities are considered viable when their optical density remains higher (95% confidence) than that of wells that were not inoculated for two transfer cycles. The frequency of cases in which the local community at a given site was viable is indicated by blue shading. The orange box locates the conditions in the uniformly degraded landscape of phase 2 of the experiment. (A) At the start of phase 1: concentrations of <0.15 g/L Dalapon are benign; a few communities persist in sublethal concentrations of up to 0.55 g/L Dalapon; no communities survive the lethal concentrations of 0.65 g/L Dalapon or greater. (B) At the end of phase 1: an increasing proportion of the landscape is occupied by viable communities. (C) Phase 2: The majority of communities that thrived on the uniformly degraded landscape had previously evolved in intermediate levels of Dalapon.



**Fig. 3.** The rate of community range expansion during selection (phase 1). The rate is calculated as the slope of landscape occupancy over time as number of transfers between the two first transfers and the two last transfers. No dispersal was done for the last three transfers. The percent landscape occupied was calculated as the ratio of the number of cells with viable communities over the total number of cells receiving a specific range of Dalapon concentrations (benign, sublethal, or lethal). The bars indicate mean values and 95% confidence intervals. In benign conditions (0–0.15 g/L Dalapon), viable communities already occupied most available sites, so that little increase in landscape occupancy was possible. In more stressful sublethal conditions (0.25–0.55 g/L Dalapon), dispersal is necessary for communities to spread rapidly into polluted sites. In lethal conditions (0.65–1.50 g/L Dalapon), dilution of the initial inoculum, and the concomitant reduction of initial diversity, restricted the spread of viable communities.

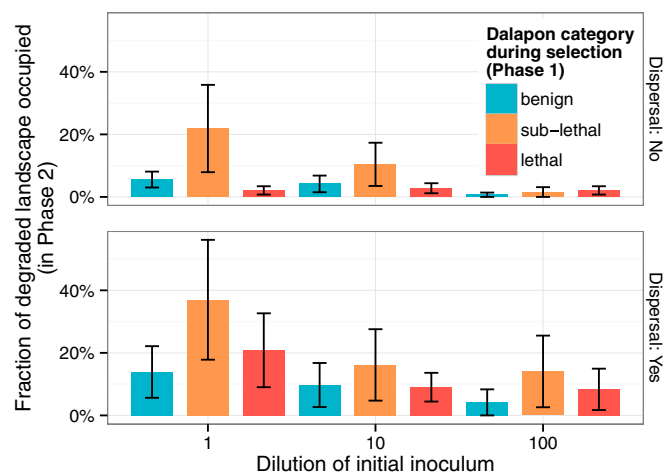
**Phase 2.** During phase 2, the entire metacommunity was exposed to a uniformly degraded landscape in which conditions in all wells were lethal to the source soil communities at the start of phase 1 (0.65 g/L of Dalapon and 2 g/L glucose, as indicated by the orange square in Fig. 2). The frequency of rescue was affected by all of the treatments (Fig. 2C and Table S2; general linear model; main effects for dilution  $\chi^2_{1,60} = 6.368$ ,  $P = 0.014$ ; dispersal  $\chi^2_{1,60} = 8.6340$ ,  $P = 0.003$ ; Dalapon category  $\chi^2_{2,60} = 5.495$ ,  $P = 0.006$ ). The majority of communities that thrived on the degraded landscape evolved in intermediate levels of Dalapon [Figs. 2C and 3; mean across four source communities of 62% (57.2–65.0%) of viable communities after landscape degradation had previously evolved in sublethal conditions during phase 1]. Although glucose concentration did affect the density of local communities during selection (Fig. S1A and B), the frequency of rescue was not related to glucose concentration (Fig. S1C), suggesting that microorganisms abundant at high glucose concentrations were not responsible for community rescue. The overall frequency of rescue was reduced by dilution of the source community (a decrease of 6% of landscape occupied after degradation with every  $\log_{10}$  increment of dilution), indicating that dilution eliminated rare types that were involved in community rescue. Finally, dispersal among local communities, before abrupt exposure to severe stress, was again the key factor governing the probability of community rescue, allowing local communities to recover in regions of the landscape that were lethal to the source communities. Hence, the fraction of the landscape occupied by viable communities at the end of phase 2 depended on the history of exposure of a local community, its initial diversity, and the connection of local communities in the metacommunity by dispersal (Fig. 4 and Table S2).

**Community Composition.** Local communities that recovered after exposure to lethal concentrations of Dalapon had diversity levels comparable to those of source communities (no differences

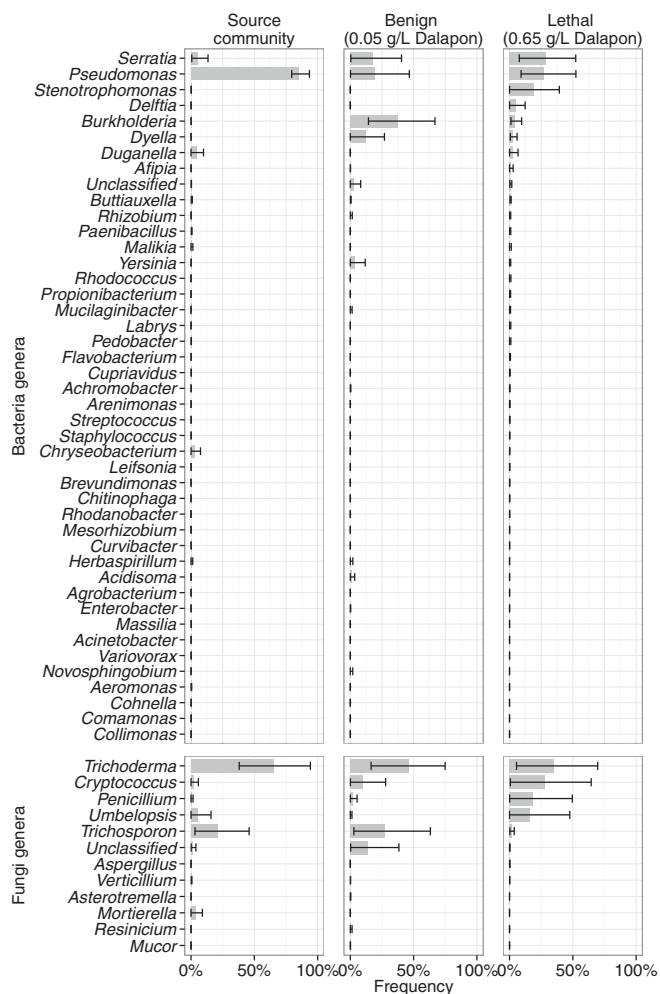
between source, benign-adapted or lethal-adapted communities in Shannon diversity based on OTU counts, ANOVA,  $F_{2,29} = 0.722$   $P = 0.49$ ; >43 OTUs and >38 genera in each adapted community; Fig. 1), but their composition differed strongly from that of the source community for both bacteria and fungi [Fig. 5; mean turnover between source and lethal adapted communities based on Shannon beta-diversity calculated for OTUs of 56% (17.3–81.1%) (14)].

Among both bacteria and fungi, the evolved communities often retained the taxa that dominated the source communities but also recruited other taxa that were initially rare or undetectable. Among bacteria, *Pseudomonas*, a genus with exceptionally high metabolic diversity (15), and *Serratia* dominated all source communities [mean proportion of total sequences in an assay (95% confidence limits); *Pseudomonas* mean 84.9% (79.5–93.5%); *Serratia* 5.0% (0.5–5.0%)] and all viable communities evolved in lethal conditions [*Pseudomonas* 27.3% (8.9–49.5%); *Serratia* 28.7 (7.7–52.1%)] (Fig. 5). In benign conditions, *Serratia* became more prominent, and several genera that were very rare or undetectable in the source community became much more abundant, in particular *Burkholderia* [from 0.07% (0.02–0.11%) in sources to 37.9% (8.8–64.4%) in communities adapted to benign conditions], *Dyella* [from undetectable to 12.4% (0.0–26.9%)] and *Yersinia* [from 0.04% (0.01–0.08%) to 4.0% (0.00–11.8%)]. These taxa persisted, although they became less frequent, in viable communities adapted to lethal conditions, where a new suite of bacteria increased in frequency from undetectable levels, including *Stenotrophomonas* [from 0.08% (0.00–0.25%) in sources to 19.4% (0.02–40.0%) in communities adapted to lethal conditions] and *Delftia* [from undetectable to 4.8% (0.00–12.3%)]. The most dominant bacteria in the initially lethal conditions were all from the Gammaproteobacteria class (*Serratia*, *Pseudomonas*, *Stenotrophomonas*, and the less common *Dyella*). *Burkholderia* and *Duganella*, which were also present in the initially lethal conditions, are from the related class Betaproteobacteria.

Among fungi, source and evolved communities were on average dominated by *Trichoderma* [mean across all communities of 46.8% (28.0–65.5%)]. *Trichosporon* was important in source and benign communities [mean across source and benign communities of 52.5% (29.3–75.5%)]. These persisted in at least



**Fig. 4.** The proportion of the uniformly degraded landscape (0.65 g/L Dalapon and 2.00 g/L glucose) occupied by rescued communities at the end of phase 2. The bars indicate mean values and 95% confidence intervals. Local communities that experienced intermediate sublethal levels of stress (0.25–0.55 g/L Dalapon) during phase 1 are more likely to be rescued, and thus occupy a larger proportion of the degraded landscape than communities that experienced benign conditions (0–0.15 g/L Dalapon), and hence did not evolve resistance, or communities that experienced severe stress (0.65–1.50 g/L Dalapon), and hence supported only very small populations.



**Fig. 5.** Genera in source and evolved communities. Genera found in more than one sample are presented and ordered by mean frequency in the high-Dalapon selection environment. The bars indicate mean values and 95% confidence intervals. Sequences that could not be resolved to genus were labeled as "unclassified."

some communities in lethal conditions, where they were joined by *Penicillium* [from 0.7% (0.04–1.57%) in sources to 18.8% (0.01–49.7%) in communities adapted to lethal conditions]. *Trichoderma* and *Penicillium* are of the phylum Ascomycota, but *Trichosporon* is of the phylum Basidiomycota.

## Discussion

**Process of Evolutionary Rescue.** Viable communities containing a diversity of species were found to thrive in conditions lethal to the original community and its constituent organisms, demonstrating community rescue.

Plastic responses and sorting of existing rare and resistant types cannot explain our results. A Dalapon concentration of  $\geq 0.65$  g·L<sup>-1</sup> was lethal to initial communities and all their constituent species (Fig. 2). It remains lethal in metacommunities without dispersal, and many transfers are required before persistent host communities appear in metacommunities with dispersal. Because the time to adaptation to the lethal conditions is much greater than the generation time of the organisms in our communities, plastic changes within species are not sufficient to withstand this degree of environmental degradation, even when a more gradual acclimation is possible through dispersal across the gradient of conditions. The source communities were thus not resistant to high Dalapon concentrations [community resistance:

the maintenance of species composition when a community faces a disturbance (11)]. The recovery of communities when dispersal is allowed shows that some species have adapted to somewhat lower concentrations and as a consequence can undergo evolutionary rescue when they are subsequently transferred to initially lethal conditions. The adapting species may have gained their new ability to withstand initially lethal conditions through novel beneficial mutations, sexual recombination, or the integration of horizontally transferred genetic elements (16, 17). Communities that recover from lethal stress have not been swept by one or a very few species but instead remain diverse, and evolutionary rescue occurs in both initially common types and initially rare types. Evolution within species may confer some level of community resilience and evolutionary resilience (13), as demonstrated by the persistence of the abundant genera *Pseudomonas*, *Serratia*, and *Trichoderma*. Initially common types have larger populations, which is favorable for rapid adaptation to stress (2).

However, population size is probably not sufficient to ensure rescue, which is likely to require preexisting physiological capacity to resist sublethal levels of stress that can be improved through adaptation to allow for survival in lethal conditions. All genera of bacteria [*Serratia* (18), *Pseudomonas* (19–23), *Stenotrophomonas* (24), *Delftia* (24, 25), and *Burkholderia* (26)] that dominate the initially lethal conditions have been identified as including species that can degrade Dalapon. Of the fungi that dominate the initially lethal conditions, species of *Trichoderma* are known to degrade chloro-organic acids (27), and species of *Penicillium* are known to be resistant to Dalapon and their frequency increases in soil communities in the presence of Dalapon (28).

Some of these genera with established capacities to degrade Dalapon or related substances were common in the initial source communities, had large population size facilitating adaptation, and remained common after degradation. A species of *Serratia* has been isolated that can degrade pentachlorophenol (18), a halogenated compound likely requiring the same degradation process as Dalapon. Some species of the genus *Pseudomonas* are known to have physiological mechanisms required for the degradation of halogenated compounds such as Dalapon. In soil communities exposed to Dalapon in chemostats (19), *Pseudomonas putida* was isolated and shown to have dehalogenase activity (20). However, selection for metabolization of Dalapon in the *P. putida* strains capable of dehalogenase activity did not lead to the capacity to use Dalapon as sole source of carbon and energy (21). Horizontal transfer of genes involved in dehalogenase activity is possible. One of the genes that is sufficient to confer dehalogenase activity in the isolates of *P. putida* is found in a mobile DNA element that can relocate from its chromosomal location to a plasmid (22). The ability to use Dalapon as a substrate was associated with conjugative plasmids in species of *Pseudomonas* and *Alcaligenes* (23). The dehalogenase gene can function readily in other organisms and can be inserted into plants to act as a selective marker (29). The mobility of these genes would be expected to increase the probability and speed of adaptation of a community of microorganisms (30).

Large population size is not essential for adaptation, which also occurred in initially rare types. Adaptation in initially rare types leads to an increase in frequency of these newly adapted types (Fig. 5). Many of the genera that dominated the communities in the lethal levels of Dalapon were initially rare in the source community (*Stenotrophomonas*, *Delftia*, and *Burkholderia*). These genera have been identified as containing species capable of degrading some toxicants. Species of *Delftia* (25) and *Burkholderia* (26) have been documented as having dehalogenase activity that would be required for the breakdown of Dalapon. Species of *Stenotrophomonas* and *Delftia* are also known to degrade atrazine (24), a herbicide that requires dehalogenase activity for degradation.

**Probability of Evolutionary Rescue.** Dispersal will facilitate adaptation to heterogeneous landscapes because it enables incompletely resistant lineages to move up a stress gradient. While they remain rare, resistant types are unlikely to be dispersed to

local communities with high levels of stress. They will expand in sites with intermediate levels of stress, however, because their evolved resistance has the correlated effect of enabling them to grow successfully at somewhat higher levels of stress. Once they have become abundant at such sites, they will be recruited at much higher rates to highly stressful sites by dispersal. Invasion of lethal sites is based on previous expansion in somewhat less stressful sites, which leads either to an increased frequency of beneficial genetic changes, which can then be dispersed, or to an increased number of dispersing individuals. The dependence of community rescue on rare types, either rare existing species undergoing adaptation or rare new genotypes within more common species arising through mutation, makes the process sensitive to stochasticity in the composition of the founding community and initial conditions, leading to dissimilar evolved communities. This stochasticity is compounded by the fact that evolutionary rescue, and by extension community rescue, is most influenced by existing diversity or by genetic changes arising early in the process (31). Furthermore, the likelihood of a given species to undergo evolutionary rescue, and thus contribute to the community rescue process, depends on its ecological interactions (7, 32), and thus on the composition of the stochastically assembled starting community. The sensitivity of the process to stochasticity makes it necessary to use high-throughput techniques to provide adequate levels of replication. The capacity of the resulting communities (Fig. 5) to reach densities comparable to those of the undisturbed communities (Fig. S1) suggests the presence of functional degeneracy [functional degeneracy or redundancy: the ability of different taxa to carry out a functional process at similar rates (11)].

Our results relate community rescue to previous work on evolutionary rescue (2, 4, 5, 7, 33), and thereby enable us to link corresponding processes at two scales, the evolutionary recovery of populations and the ecological response of communities to environmental stress. In both cases, rescue depends on the same combination of three factors. First, the community should be sufficiently diverse, so as to include rare types able to resist at least an intermediate level of stress. Second, the community should have a history of prior exposure to nonlethal levels of the stressor, so that types resistant to intermediate levels of stress have already increased in frequency and diversity, through genetic changes. This is because resistance to a stress is rarely specific to a particular dose; rather, any type that is resistant to a particular dose will also be resistant to a range of similar doses. The spread of types resistant to a certain level of stress may thereby enable the community to resist a higher level of stress when this is encountered in the future, or in another site to which individuals have dispersed. Third, there should be dispersal among local communities so that the most resistant of these preadapted types can move up the gradient of stress and thereby extend the occupied region of the landscape, allowing the rescue of the metacommunity. Our experiment has provided clear evidence for all three of these predicted effects: Community rescue was promoted by diversity (manipulated by dilution of the source communities), community rescue was more frequent among local communities that had previously experienced intermediate levels of stress, and dispersal increased the frequency of rescue in metacommunities.

A general theory of rescue, applicable to both populations and communities, and supported by firm experimental evidence, will be an essential tool for understanding and managing the likelihood of community rescue in a range of socially important contexts, including microbial communities exposed to antibiotics (34, 35), the eradication of pests in agricultural settings (36), the evolution of microbial communities for industrial processes such as bioremediation, and with further theoretical and experimental insight into the applicability to higher organisms, for the conservation of biodiversity in landscapes dominated by human activities (37).

## Methods

**The Stress: Dalapon.** Dalapon (2,2-dichloropropanoic acid, CAS-75-99-0, KEGG-C18600) is a herbicide that was once widely used. Dalapon is toxic, but some microbial communities can break it down in soil, so it represents an interesting selective agent for the study of evolutionary rescue of communities of soil microorganisms and the recovery of ecosystem processes. Natural selection acting on entire microbial communities in chemostats has already been shown to lead to the isolation of communities capable of withstanding and metabolizing Dalapon (19). Ten grams of garden soil was sufficient to lead to the isolation of a *Rhizobium* that could use Dalapon as sole carbon source (38). Growth using Dalapon as a substrate involves a dehalogenase enzyme that is required for the metabolism of a number of other chlorinated herbicides and pollutants (39, 40). Community rescue is also suspected to be important in the development of the capacity of microbial communities to degrade other halogenated compounds that are initially toxic to the community (8).

**Source Communities.** The source communities were soil (2) and sediment (2) samples from four sites in old-growth forest at Mont St-Hilaire, Quebec. The samples were taken from within the protected area of the Gault Nature Reserve of McGill University at Mont Saint-Hilaire, Quebec. The protected area is long established and exposure to herbicides is not expected at these locations. The samples were taken on the shore of Lac Hertel where streams flow in. Samples of forest soil and lake sediment were taken from Botany Bay (N 45° 32' 38.43" E 73° 8' 45.13", elevation 199 m) and North Creek delta (N 45° 32' 53.04" E 73° 9' 8.52", elevation 181 m).

**Experimental Landscape.** We set up model metacommunities in the inner 60 wells of 96-well plates where each well constituted a local community. The metacommunities were exposed to a gradient of Dalapon pollution, increasing in concentration from zero to lethal, crossed with a gradient of glucose concentration, from zero to levels consistent with high-glucose media (5 g/L), together forming a 2D landscape (Fig. 2A). Communities were cultured in chlorine-free growth medium (41) supplemented with Dalapon and glucose: Dalapon varied across the columns of the plate (with concentrations increasing from 0.05 to 0.75 g/L by 0.10 g/L intervals and a final elevated concentration of 1.5 g/L), and glucose varied across the rows of the plate (with concentrations of 5, 2, 1, 0.5, 0.25, and 0 g/L). The outer wells of the 96-well plate did not receive Dalapon, glucose, or inoculation and served as blanks in the calculation of yield. Every well on a plate was initially inoculated with microorganisms from the same source community, and the local communities responded according to the level of stress and the rate of glucose supply. We imposed a glucose gradient to modulate species abundance and population productivity. We manipulated the initial diversity of the local communities through three levels of dilution (1-, 10-, and 100-fold) of aqueous elution of the source communities. The distribution of species or types is expected to follow an approximate log distribution with an exaggerated tail of rare species (42, 43). It follows that a local community established as a small sample from the source community will contain fewer types than the source community itself, because many rare types will be missing by chance, and that replicate samples will often have different composition because each will contain some rare types but not others. Local communities were propagated by transferring them twice weekly to fresh medium using 5% of the grown community as inoculum. Dispersal among local communities was achieved during transfer by pooling samples from all wells in a vessel with 29,700  $\mu$ L of sterile medium and inoculating each well of the landscape with 5  $\mu$ L of this pooled community in addition to the 5  $\mu$ L directly transferred from corresponding well in the previous cycle. The experiment involved 48 different metacommunities (four source communities  $\times$  three dilution levels  $\times$  two dispersal treatments  $\times$  two replicates as complete blocks that were transferred alternately) and comprised 2,880 local communities.

**Phase 1: Evolution of Metacommunities on a Heterogeneous Landscape.** A small inoculum from each site was transferred to a fresh plate for a total of 14 growth cycles, equivalent to about 50 generations. The artificial landscapes were transferred twice weekly, with or without dispersal. If dispersal were continued up to and including during the second phase of the experiment, in which the whole landscape is degraded, organisms from the viable community experiencing conditions most similar to the degraded conditions would be expected to disperse to the whole landscape. This would be expected to result in uniform growth of these resistant communities across the whole homogeneously degraded landscape. To avoid this, all communities were transferred three times (11 d) without dispersal at the conclusion of

phase 1 (11 transfers with dispersal and 3 transfers without) and there was no dispersal during phase 2.

The transfers were performed by the robotic liquid handling platforms in the Laboratory for Experimental Ecology and Evolution and at the Cell Imaging and Analysis Network in the Department of Biology at McGill University. At the end of each growth cycle, in both phases, the density of microorganisms in each local community was monitored by measuring the optical density at 450 nm.

**Phase 2: Outcome of Abrupt Environmental Degradation.** In phase 2, the environment was degraded by the application of a uniform concentration of Dalapon, lethal to the source community (0.65 g/L), to all wells. Community rescue was scored when local communities recovered and persisted in the degraded landscape at the end of Phase 2.

**Community Characterization.** Community composition was established by amplicon sequencing for source communities and communities evolved in benign conditions (2 g/L glucose and 0.05 g/L Dalapon) and the viable communities evolved in lethal conditions (2g/L glucose and 0.65 g/L Dalapon) on the polluted landscape across which dispersal was enabled. DNA extraction was conducted using the Genomic Plant/Fungi DNA kit (IBI

Scientific). Amplicon sequencing was conducted by Research and Testing Laboratory on 454 platforms, using assays for bacteria and fungi identification (Table S3). Sequences were analyzed using the QIIME pipeline and associated modules (44). Pyrosequencing data were fully quality-controlled and sequences were removed if they had errors in the 10-bp barcodes (midtags) and taxon-specific primers, were <450 bp long, had low quality scores (<25), and  $\geq 7$  bp homopolymer inserts. Pyrosequences were clustered into OTUs at the 97% similarity level using USearch (45), and the associated de novo chimera checker (46) was used to detect and remove chimeras and OTUs represented by fewer than four sequences across all samples. Representative sequences from each OTU were assigned to a taxonomic group against the National Center for Biotechnology Information nonredundant nucleotide database using the BLAST algorithm (47).

**ACKNOWLEDGMENTS.** We thank Guillaume Lesage for contributing to the programming and operation of the robotic liquid handling platforms. G.B. and A.G. are supported by funding from the Natural Sciences and Engineering Research Council of Canada. The Laboratory for Experimental Ecology and Evolution and Cell Imaging and Analysis Network robotic liquid handling platforms were funded by the Canadian Foundation for Innovation. A.G. is supported by the Canada Research Chair Program.

- Samani P, Bell G (2010) Adaptation of experimental yeast populations to stressful conditions in relation to population size. *J Evol Biol* 23(4):791–796.
- Bell G, Gonzalez A (2009) Evolutionary rescue can prevent extinction following environmental change. *Ecol Lett* 12(9):942–948.
- Agashe D, Falk JJ, Bolnick DI (2011) Effects of founding genetic variation on adaptation to a novel resource. *Evolution* 65(9):2481–2491.
- Bell G, Gonzalez A (2011) Adaptation and evolutionary rescue in metapopulations experiencing environmental deterioration. *Science* 332(6035):1327–1330.
- Gonzalez A, Bell G (2013) Evolutionary rescue and adaptation to abrupt environmental change depends upon the history of stress. *Philos Trans R Soc Lond B Biol Sci* 368(1610):20120079.
- Carlson SM, Cunningham CJ, Westley PA (2014) Evolutionary rescue in a changing world. *Trends Ecol Evol* 29(9):521–530.
- Fussmann GF, Gonzalez A (2013) Evolutionary rescue can maintain an oscillating community undergoing environmental change. *Interface Focus* 3(6):20130036.
- van der Meer JR, de Vos WM, Harayama S, Zehnder AJ (1992) Molecular mechanisms of genetic adaptation to xenobiotic compounds. *Microbiol Rev* 56(4):677–694.
- de Mazancourt C, Johnson E, Barraclough TG (2008) Biodiversity inhibits species' evolutionary responses to changing environments. *Ecol Lett* 11(4):380–388.
- Norberg J, Urban MC, Vellend M, Klausmeier CA, Loeuille N (2012) Eco-evolutionary responses of biodiversity to climate change. *Nat Clim Chang* 2:747–751.
- Allison SD, Martiny JBH (2008) Colloquium paper: Resistance, resilience, and redundancy in microbial communities. *Proc Natl Acad Sci USA* 105(Suppl 1):11512–11519.
- Thrush SF, et al. (2009) Forecasting the limits of resilience: Integrating empirical research with theory. *Proc Biol Sci* 276(1671):3209–3217.
- Sgrò CM, Lowe AJ, Hoffmann AA (2011) Building evolutionary resilience for conserving biodiversity under climate change. *Evol Appl* 4(2):326–337.
- Charney N, Record S (2013) Jost diversity measures for community data, package "vegetarian" (Amherst, MA).
- Palleroni NJ (2010) *Pseudomonas*. *Topley and Wilson's Microbiology and Microbial Infections*, eds Mahy BWJ, et al. (Wiley, Chichester, UK).
- Syvanen M (2012) Evolutionary implications of horizontal gene transfer. *Annu Rev Genet* 46:341–358.
- Fitzpatrick DA (2012) Horizontal gene transfer in fungi. *FEMS Microbiol Lett* 329(1):1–8.
- Singh S, Chandra R, Patel DK, Rai V (2007) Isolation and characterization of novel *Serratia marcescens* (AY927692) for pentachlorophenol degradation from pulp and paper mill waste. *World J Microbiol Biotechnol* 23(12):1747–1754.
- Senior E, Bull AT, Slater JH (1976) Enzyme evolution in a microbial community growing on the herbicide Dalapon. *Nature* 263(5577):476–479.
- Weightman AJ, Slater JH, Bull AT (1979) The partial purification of two dehalogenases from *Pseudomonas putida* PP3. *FEMS Microbiol Lett* 6:231–234.
- Weightman AJ, Slater JH (1980) Selection of *Pseudomonas putida* strains with elevated dehalogenase activities by continuous culture growth on chlorinated alkanic acids. *Microbiology* 121:187–193.
- Thomas AW, Topping AW, Slater JH, Weightman AJ (1992) Localization and functional analysis of structural and regulatory dehalogenase genes carried on DEH from *Pseudomonas putida* PP3. *J Bacteriol* 174(6):1941–1947.
- Hardman DJ, Gowland PC, Slater JH (1986) Large plasmids from soil bacteria enriched on halogenated alkanic acids. *Appl Environ Microbiol* 51(1):44–51.
- Sadowsky MJ (2010) Diversity and evolution of micro-organisms and pathways for the degradation of environmental contaminants: A case study with the s-triazine herbicides. *Ecology of Industrial Pollution*, eds Batty LC, Hallberg KB (Cambridge Univ Press, Cambridge, UK), pp 205–225.
- Sota M, Endo M, Nitta K, Kawasaki H, Tsuda M (2002) Characterization of a class II defective transposon carrying two haloacetate dehalogenase genes from *Delftia acidovorans* plasmid pUO1. *Appl Environ Microbiol* 68(5):2307–2315.
- Kurihara T, Yamauchi T, Ichiyama S, Takahata H, Esaki N (2003) Purification, characterization, and gene cloning of a novel fluoroacetate dehalogenase from *Burkholderia* sp. FA1. *J Mol Catal, B Enzym* 23:347–355.
- Jensen HL (1957) Decomposition of chloro-organic acids by fungi. *Nature* 180(4599):1416.
- Hirsch P, Alexander M (1960) Microbial decomposition of halogenated propionic and acetic acids. *Can J Microbiol* 6(3):241–249.
- Buchanan-Wollaston V, Snape A, Cannon F (1992) A plant selectable marker gene based on the detoxification of the herbicide dalapon. *Plant Cell Rep* 11(12):627–631.
- Frost LS, Leplae R, Summers AO, Toussaint A (2005) Mobile genetic elements: The agents of open source evolution. *Nat Rev Microbiol* 3(9):722–732.
- Kirkpatrick ME, Peischl S (2013) Evolutionary rescue by beneficial mutations in environments that change in space and time. *Philos Trans R Soc Lond B Biol Sci* 368(1610):20120082.
- Osmond MM, de Mazancourt C (2013) How competition affects evolutionary rescue. *Philos Trans R Soc Lond B Biol Sci* 368(1610):20120085.
- Gonzalez A, Ronce O, Ferriere R, Hochberg ME (2013) Evolutionary rescue in changing environments. *Philos Trans R Soc Lond B Biol Sci* 368(1610):20120404.
- Sommer MO, Dantas G (2011) Antibiotics and the resistant microbiome. *Curr Opin Microbiol* 14(5):556–563.
- Hochberg ME, Jansen G (2015) Bacteria: Assessing resistance to new antibiotics. *Nature* 519(7542):158.
- Neve P, Busi R, Renton M, Vila-Aiub MM (2014) Expanding the eco-evolutionary context of herbicide resistance research. *Pest Manag Sci* 70(9):1385–1393.
- Kinnison MT, Hairston NG (2007) Eco-evolutionary conservation biology: Contemporary evolution and the dynamics of persistence. *Funct Ecol* 21:444–454.
- Berry EKM, Allison N, Skinner AJ, Cooper RA (1979) Degradation of the selective herbicide 2,2-dichloropropionate (Dalapon) by a soil bacterium. *J Gen Microbiol* 110:39–45.
- Middeldorp PJM, et al. (1999) Anaerobic microbial reductive dehalogenation of chlorinated ethenes. *Bioremediat J* 3(3):151–169.
- Furukawa K (2003) 'Super bugs' for bioremediation. *Trends Biotechnol* 21(5):187–190.
- Kröckel L, Focht DD (1987) Construction of chlorobenzene-utilizing recombinants by progenitive manifestation of a rare event. *Appl Environ Microbiol* 53(10):2470–2475.
- McGill BJ, et al. (2007) Species abundance distributions: Moving beyond single prediction theories to integration within an ecological framework. *Ecol Lett* 10(10):995–1015.
- Volkov I, Banavar JR, Hubbell SP, Maritan A (2003) Neutral theory and relative species abundance in ecology. *Nature* 424(6952):1035–1037.
- Caporaso JG, et al. (2010) QIIME allows analysis of high-throughput community sequencing data. *Nat Methods* 7(5):335–336.
- Edgar RC (2010) Search and clustering orders of magnitude faster than BLAST. *Bioinformatics* 26(19):2460–2461.
- Edgar RC, Haas BJ, Clemente JC, Quince C, Knight R (2011) UCHIME improves sensitivity and speed of chimera detection. *Bioinformatics* 27(16):2194–2200.
- Altschul SF, Gish W, Miller W, Myers EW, Lipman DJ (1990) Basic local alignment search tool. *J Mol Biol* 215(3):403–410.