

Black fly larvae facilitate community recovery in a mountain stream

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SUMMARY

1. Early colonising ecosystem engineers modify habitats and alter the abundance of basal resources following disturbances. These changes can have profound effects on ecosystem recovery via facilitative or inhibitory effects on subsequent colonists.
2. We quantified how black fly larvae, which can be pioneer species during secondary succession in streams, influence initial community recovery following a simulated drying disturbance.
3. Black fly larvae anchor themselves to the stream substratum with silk, and diatoms adhere to the silk of black flies. Therefore, we hypothesised that black flies speed community recovery following disturbances by increasing the accrual rate of basal resources with their silk.
4. We compared algal and detrital resource abundance and invertebrate community recovery on recently submerged cobbles across three treatments: increased black fly abundance, added black fly silk plus ambient black fly abundance and ambient black fly abundance (control).
5. After 24 h, the increased black fly treatment had more chlorophyll *a*, detritus and greater invertebrate abundance and richness, and replicates had more self-similar communities than the control treatment.
6. The added silk treatment responded similarly to the increased black fly treatment, supporting the hypothesis that black flies increase the rate of basal resource accrual with their silk, increasing the colonisation rates of other invertebrate species.
7. Our study suggests that black flies are akin to other organisms that facilitate recovery following disturbance (e.g. alders fixing nitrogen following glacial retreat). Further research is needed to determine the effect of black flies on long-term patterns of recovery and the applicability of our results to natural disturbances in streams.

Keywords: community recovery, disturbance, ecosystem engineer, secondary succession, Simuliidae

Introduction

Community development following perturbations, both during primary and secondary succession, is among the most widely studied processes in ecology. Pioneer species may play a key role if they act as ecosystem engineers by modifying physical habitat or altering basal resources (Jones, Lawton & Shachak, 1997). For example, early colonising alders (*Alnus* spp) facilitate primary succession by fixing nitrogen in newly exposed landscapes following glacial retreat, thus improving abiotic conditions for other colonising plant

species (Crocker & Major, 1955; Chapin *et al.*, 1994). Birds are thought to speed secondary succession following disturbance of forests by enhancing seed dispersal (Gorchov *et al.*, 1993). Early colonising ecosystem engineers can also exert inhibitory effects on colonisation, or facilitative and inhibitory effects can offset one another. For example, allelopathy by heathers (*Calluna* spp) inhibits the colonisation of conifers following fires (Mallik, 2003), while lupins (*Lupinus* spp) exert both positive and negative effects on subsequent colonists following volcanic eruptions (Morris & Wood, 1989).

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Analogous examples of early colonising ecosystem engineers from freshwater ecosystems are scarce, despite the prevalence of disturbance in streams. Many studies have described ecosystem recovery from disturbance during secondary succession in streams (e.g. Fisher *et al.*, 1982; Boulton *et al.*, 1992; Stanley, Powers & Lottig, 2010), and several have described colonisation by lotic organisms during primary succession (e.g. Milner *et al.*, 2011). Drying disturbance is thought to be of particular importance in stream ecosystems, as changes in discharge cause frequent cycles of community loss and recovery (Wallace, 1990; Yount & Niemi, 1990; Lake, 2000). Many ecosystem engineers have been documented in lotic ecosystems, including vertebrates (e.g. beavers, salmon) and invertebrates (e.g. mussels and caddisflies; Moore, 2006), and may play a key role in stream community recovery. For example, Ledger *et al.* (2006) demonstrated that remnant populations of snails acted as ecosystem engineers by bulldozing epilithon to influence community composition. Cardinale, Smith & Palmer (2001) found that a hydropsychid caddisfly increased the rate of invertebrate colonisation of gravel baskets, although it was unclear whether this effect was through ecosystem engineering. Here, we examine the influence of an early colonising ecosystem engineer on the initial stages of stream community recovery following a simulated drying disturbance.

Black fly larvae (Diptera: Simuliidae) are typically among the earliest colonists of recently submerged or scoured substrata in streams and rivers (e.g. Malmqvist *et al.*, 1991; Matthaei *et al.*, 1996; Bogan, Boersma & Lytle, 2013). Larvae anchor themselves to objects in flowing water using silk (Reidelbach & Kiel, 1990), and this silk has been shown to increase the rate of diatom adherence to glass slides (Kepcija *et al.*, 2006; Supporting Information Figure S1). Detritus may adhere to silk as well, and both diatoms and detritus are essential basal resources in streams (e.g. Eggert & Wallace, 2003; Layer, Hildrew & Woodward, 2013). We hypothesised that silk deposited by early colonising black fly larvae increases the rate of resource accumulation on recently submerged substrata, providing food for greater numbers of subsequent colonists and speeding community recovery. That is, black flies act as early colonising ecosystem engineers by transferring resources from the water column to the stream bed, increasing their availability to benthic macroinvertebrate colonists (Jones *et al.*, 1997). Alternatively, because black flies compete aggressively for space (Wiley & Kohler, 1981; Dudley, D'Antonio & Cooper, 1990), larvae may inhibit colonisation, and subsequent community recovery, through interference competition.

To distinguish between these two hypotheses, we compared basal resource accumulation and invertebrate community recovery on newly submerged cobbles in a montane stream across three treatments: (i) increased black fly abundance, (ii) added black fly silk and ambient black fly abundance and (iii) ambient black fly abundance (control). A comparison between the increased and ambient black fly abundance would reveal the influence of black flies on invertebrate and algal colonisation and detrital accumulation. We included the added silk treatment to examine whether its deposition could be a mechanism by which black flies influence community recovery (i.e. by comparing the silk and control treatments) and to determine whether any positive effects of silk are offset by interference competition from the black flies (i.e. if greater invertebrate abundance is observed in the silk than the black fly treatment).

Methods

Field work was conducted in Convict Creek, California (altitude 2200 m), from 18 August to 13 September 2012, in the grounds of the Sierra Nevada Aquatic Research Laboratory (37°36'57"N, 118°49'47"W). Convict Creek is a cobble-bottomed, low-gradient (slope *c.* 2%), montane trout stream. We quantified how black flies (*Simulium*) and their silk affect algal abundance (using chlorophyll *a* as a proxy), detritus accumulation, and invertebrate richness, abundance, and community composition on recently submerged substrata, because increases in these variables are associated with community recovery in lotic systems (e.g. Fisher *et al.*, 1982; Doeg, Lake & Marchant, 2006). We conducted the experiment in plastic channels (0.18 m wide × 1.38 m long × 0.17 m high) placed in the stream on a concrete slab. Channels were open to the stream at the up and downstream ends and contained previously dry cobbles collected from the floodplain of Convict Creek. Using dry substrata from the floodplain, our aim was to simulate stream recovery following a drying disturbance.

We blocked for time to account for changes in the stream during the month-long experiment. The experimental design included five 'temporal blocks' with two replicates of each of the three treatments per block. This resulted in six plastic channels per block and 10 replicates of each of the three treatments (30 plastic channels total). Each temporal block lasted 24 h, beginning and ending at 9 am (i.e. each channel was in the stream for 24 h). For each block, we filled six buckets with stream water and collected (dry) cobbles from the floodplain beside Convict Creek (one bucket per channel, each with

c. seven cobbles). Then, we collected 2000 black flies from Convict Creek, dividing them equally among four buckets (two buckets each for the black fly and silk treatments, 500 black flies per bucket), while two buckets received no black flies (control buckets). During the c. 3-h collection process (lasting from c. 5:30–8:30 am), we kept counts in each of the four treatment buckets similar to ensure that cobbles in each treatment bucket were equally exposed to black fly larvae. We then randomly assigned the three treatments to each of the six channels.

At 9 am, we placed c. six cobbles in the upstream half of each plastic channel (channel surface area: 0.12 m²), providing substratum for colonisation by invertebrates. The seventh cobble, which was approximately prism-shaped, was placed in the lower half of each channel to use for quantifying chlorophyll *a*. Cobbles for the control and black fly treatments were moved directly from the buckets into their respective plastic channels. Both pads and strands of silk were visible on the cobbles exposed to black flies. For the silk treatment, we used cobbles from two of the black fly buckets, but we carefully removed all black flies from the cobbles with forceps before placing them into the channels, leaving any silk undisturbed. Thus, cobbles used in the silk treatment were exposed to black flies and their silk secretion for c. 3.5 h. The addition of 500 black fly individuals to each black fly treatment channel resulted in an initial density of 2013 *Simulium* m⁻², within the range of black fly densities observed 1 day after disturbance in another montane stream (Matthaei *et al.*, 1996). An additional treatment with no black flies would have been desirable (i.e. a treatment with no added or ambient black flies), but it was not feasible to exclude black flies while allowing diatoms, other invertebrates and detritus to enter the channels unimpeded.

At sunset on day 1 of each block, we removed the prism-shaped cobble from the lower half of each channel for chlorophyll *a* quantification. By initialising each block in the morning and removing the cobble at sunset, our aim was to allow diatoms to colonise the cobble before herbivores began immigrating into the channels during the night (invertebrate herbivore drift is largely nocturnal during the summer in Convict Creek; Hammock, Krigbaum & Johnson, 2012). We removed periphyton from the prism-shaped cobble by scrubbing with a nylon brush and rinsing with tap water. After scrubbing, we measured the dimensions (length, width and height) of each cobble, vacuum-filtered the rinsate onto a glass-fibre filter and froze the filter. We analysed the filters for chlorophyll *a* using standard fluorometric methods

(Clesceri, Greenberg & Eaton, 1998) and calculated density of chlorophyll *a* assuming that the cobbles were prism-shaped.

At 9 am on day 2 (24 h after the start of each block), we measured water velocity at the upstream end of each channel using a Marsh McBirney Flo-Mate velocity metre (water velocity range 0.25–0.57 m s⁻¹). After measuring velocity, we attached nets (mesh size: 300 µm) to the back of each channel and manually scraped the surfaces of cobbles and channel walls, allowing the current to carry channel contents into the net. Invertebrates and detritus were rinsed from each net and preserved in 70% ethanol. We waited until morning to collect invertebrates so that channels could experience one night of high drift rates and colonisation potential. We did not allow colonisation to proceed for longer than 24 h for two reasons. First, in a preliminary week-long experiment, high colonisation rates of black flies into the control channels and emigration of black flies from the black fly channels homogenised our treatments, preventing us from determining whether black flies affect community recovery (B.G. Hammock, unpublished data). Second, substantial community recovery from disturbance has been shown to occur within 24 h in other montane streams (Matthaei *et al.*, 1996), so we considered 24 h to be a relevant time scale.

We identified invertebrates to the lowest feasible taxonomic resolution (usually genus or species) and measured ash-free dry mass of the detritus in each of the channels. The ash-free dry mass was determined by drying samples at 50 °C for 48 h and then measuring the difference in mass before and after ashing for 1 h at 550 °C. Halfway through the month-long experiment, we collected kick samples (area = 0.12 m², mesh size = 500 µm) at five haphazardly selected riffle habitats between 50 and 200 m upstream of the experimental site (none of the experimental blocks were in the water at this time). We identified the invertebrates in these samples so that we could calculate the extent of recovery that occurred within 24 h (in terms of invertebrate abundance and richness) and to determine whether black flies act as pioneer species in Convict Creek as predicted (i.e. achieved higher relative abundance and densities on disturbed substrata than in the surrounding stream).

We used multimodel inference to analyse the univariate data (Burnham & Anderson, 2002). Sets of five statistical models were built for chlorophyll *a* (µg channel⁻¹), taxon richness (invertebrate taxa channel⁻¹) and detritus (mg channel⁻¹), and we compared each model set with Akaike's information criterion corrected for small sample size (AIC_c, Burnham & Anderson, 2002). The model

sets included: (i) an intercept-only model, (ii) a model with an intercept plus a parameter for black fly presence, (iii) a model with an intercept plus a parameter for silk, (iv) a model with an intercept plus a parameter for control and (v) a model with parameters for control, black flies and silk. Thus, our analysis could account for any combination of treatment effects, ranging from little effect of black flies or silk (i.e. the intercept model) to large differences among all three treatments (i.e. the full model). We used Poisson distributions of error for the richness models and Gaussian distributions of error for the chlorophyll *a* and detritus models, and built the models using the lme4 package in R 2.14.1 (Bates *et al.*, 2011; R Development Core Team, 2011). We included the temporal blocks in the models as a random effect to account for possible changes during the month-long experiment. Total invertebrate count (non-black fly invertebrates channel⁻¹) was modelled similarly, but we used the gamma-Poisson distribution rather than the Poisson to account for overdispersion (Crawley, 2007) and used 'day' as a fixed effect in the five models because the number of invertebrates appeared to decrease roughly linearly during the course of the experiment. We also included a sixth, intercept-only, model to determine whether the effect of day was predictive. We fitted the gamma-Poisson models using maximum likelihood estimation in the R statistical package bbmle (Bolker, 2010). We determined whether water velocity improved the models by comparing the best model for each of the four response variables to the same model with velocity as a predictor. We excluded *Simulium* from all statistical analyses because we manipulated its density as an experimental treatment. Using multimodel inference, our aim was to avoid some of the problems associated with null hypothesis significance testing (Anderson, Burnham & Thompson, 2000).

We tested for differences in community composition (using Bray–Curtis distance) among the black fly, silk and control groups with a multiresponse permutation procedure (Mielke & Berry, 2001) and visualised community differences using non-metric multidimensional scaling. In addition to group distinctness and ordination analyses, we also calculated the average Bray–Curtis distance of each sample replicate to each group's centroid in full multivariate space, examined the variances for these distances (i.e. dispersions) and tested whether multivariate dispersion differed by group using permutation tests (Anderson, 2006; Anderson, Ellingsen & McArdle, 2006). Finally, the Pearson's correlation values of each taxon with the ordination axes were examined to evaluate which taxa were driving the observed shifts

in community composition. We conducted ordination and multiresponse permutation procedures using PC-ORD (McCune & Mefford, 1999), while tests for homogeneity of multivariate dispersion were implemented using the vegan package in R (Oksanen *et al.*, 2012).

Results

Most of the 500 black flies that were added to the experimental channels apparently remained in place during each 24 h block, as the mean abundance of *Simulium* larvae in the black fly treatment was 475 (SE = 27), while mean abundances in the silk and control treatments were 56 (SE = 8) and 38 (SE = 7), respectively. *Simulium* was the most common taxon found in all three treatments, including the control treatment in which no black flies were added. The relative abundance and density of black flies in the control channels was 19 and 4.8 times higher than in the five benthic samples collected from riffles in Convict Creek, respectively.

Chlorophyll *a* was 4.5 and 6.8 times higher in the black fly and silk treatments, respectively, than in the control channels (Fig. 1a). The top-ranked model for chlorophyll *a* included a separate parameter for each of the three treatments (Table 1). However, the second-ranked model, which had a single parameter for the combined effect of black flies and silk, also received substantial AIC_c weight (0.39; Table 1). This indicates that while both black flies and silk predictably raised chlorophyll *a*, there was not a substantial difference between the black fly and silk treatments (i.e. 4.5 versus 6.8 times higher than control). Neither of the parameter estimates for the effects of black flies and silk on chlorophyll *a* overlapped zero, and both were positive—the black fly parameter estimate was 16.4 (95% CI: 6.2–26.5), and the silk parameter estimate was 26.6 (95% CI: 16.5–36.7; Table S1). Thus, both silk and black flies consistently increased chlorophyll *a* in our experiment.

Black flies increased the ash-free dry mass of detritus twofold (Fig. 1b). While the effect of silk on detritus was also positive (detritus was 1.3 times higher in the silk treatment than the control), the best model only included a separate parameter for the effect of black flies (Table 1). Thus, the top-ranked model did not distinguish between the silk and control treatments. For this model, the parameter estimate for the effect of black flies on detritus was 55.8 (95% CI: 28.5–83.1; Table S2).

Invertebrate abundance (all taxa besides *Simulium*) was two times higher in the black fly treatment than in the control and 1.7 times higher in the silk treatment than in the control (Fig. 2a). The top-ranked invertebrate

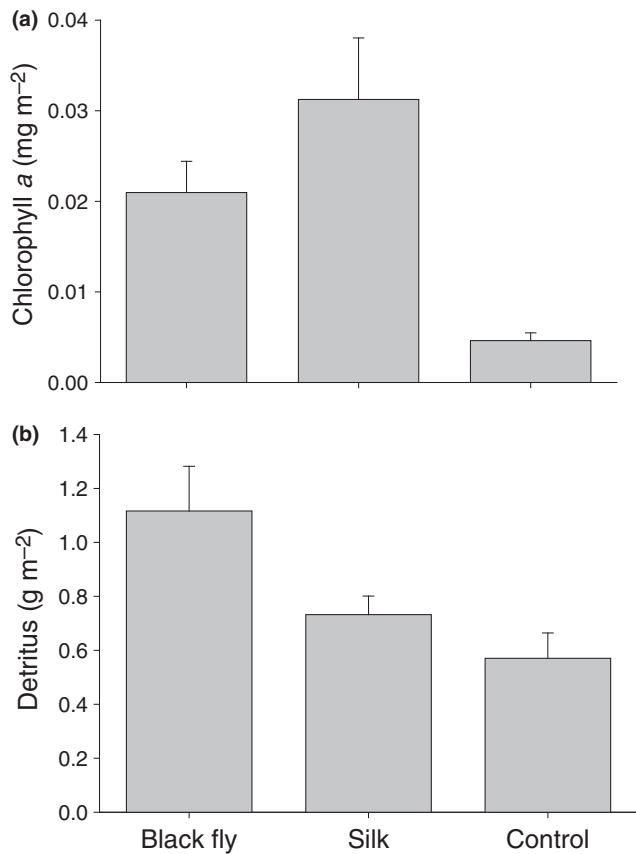


Fig. 1 The mean (\pm SE) biomass of (a) chlorophyll and (b) detritus for each treatment. Error bars include variance due to the effect of time during the month-long experiment.

Table 1 Δ AIC_c and AIC_c weight for the modelling of chlorophyll *a*, detritus and taxon richness for the Convict Creek experiment. All models include 'day' as a random effect (i.e. the temporal blocks). In the models, 'a' refers to the intercept and 'b', 's', and 'c' refer to the black fly, silk and control parameters, respectively

Fixed effects	Chl <i>a</i>		Detritus		Richness	
	Δ AIC _c	AIC _c wt	Δ AIC _c	AIC _c wt	Δ AIC _c	AIC _c wt
~ a + b + s	0	0.58	1.4	0.32	2.7	0.14
~ a + c	0.8	0.39	6	0.032	0	0.53
~ a + b	15.3	0	0	0.64	3.6	0.09
~ a + s	5.6	0.04	11.9	0	3.8	0.08
~ a	12.8	0	9.7	0.01	2.4	0.16

Δ AIC_c difference between model of interest and top-ranked model in terms of Akaike's information criterion corrected for small sample size, AIC_c wt Akaike weight.

abundance model included a separate parameter for each of the three treatments and the effect of 'day' (Table 2). For this model, the black fly parameter estimate was 0.71 (95% CI: 0.49–0.94), and the silk parameter estimate was 0.52 (95% CI: 0.29–0.75; Table S3),

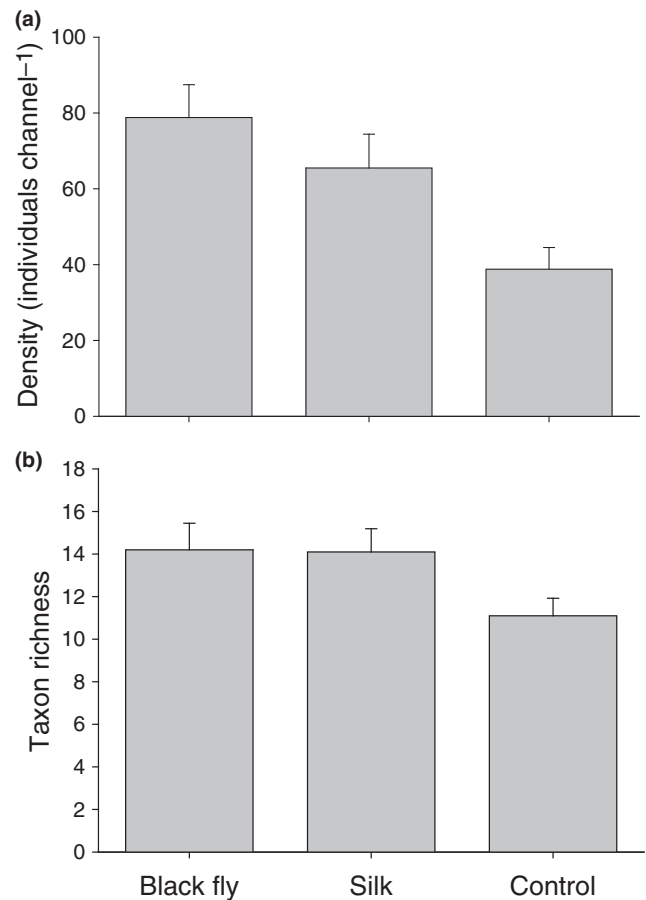


Fig. 2 The mean (\pm SE) (a) density of invertebrates (other than blackflies) and (b) taxon richness per channel by treatment. Error bars include variance due to a significant effect of time during the month-long experiment.

Table 2 Δ AIC_c and AIC_c weight for the modelling of total invertebrate abundance for the Convict Creek experiment. All models have gamma-Poisson distributions of error. In the models, 'a' refers to the intercept and 'b', 's' and 'c' refer to the black fly, silk and control parameters, respectively, 'day' refers to the temporal blocks, included as a fixed effect

Fixed effects	Δ AIC _c	AIC _c wt
~ a + b + s + day	0	0.69
~ a + c + day	1.6	0.31
~ a + b + day	13.4	<0.001
~ a + day	23.4	<0.001
~ a + s + day	24.2	<0.001
~ a	39.9	<0.001

Δ AIC_c difference between model of interest and top-ranked model in terms of Akaike's information criterion corrected for small sample size, AIC_c wt Akaike weight.

indicating that the effect of both black flies and silk on abundance is consistently positive. The 'day' parameter estimate was -0.03 (95% CI: -0.04 to -0.02), as

abundance decreased through time (Table S3). The model with a single parameter for the combined effect of black flies and silk also received substantial AIC_c weight (0.31; Table 2). For this model, the 'control' parameter was consistently negative -0.62 (95% CI: -0.83 to -0.40 ; Table S3). Thus, while black flies and silk both increase invertebrate abundance, we are uncertain as to whether there is a reliable difference between the black fly and silk treatments.

Both the black fly and silk treatments had an average of three more taxa per channel than the control treatment (Fig. 2b). The top-ranked invertebrate richness model included a single parameter for the silk and black fly treatments combined (the intercept), and a separate parameter for the control treatment (Table 1). The 95% confidence interval of the control parameter, estimated as -0.24 , did not overlap zero (95% CI: -0.46 to -0.02 ; Table S4). However, while black flies and silk appeared to increase taxon richness consistently, it should be noted that the intercept model also received some AIC_c weight (0.16; Table 1). Including water velocity as a predictor did not improve any of the univariate models.

There was a significant difference in community composition among the black fly, silk and control groups using multiresponse permutation procedure tests ($A = 0.05$, $P = 0.006$; Fig. 3). Based on Bonferroni-corrected pairwise comparisons, the black fly and control groups were compositionally distinct ($A = 0.08$, $P = 0.001$; also see Fig. 3), while the silk treatment was marginally distinct from the control ($A = 0.03$, $P = 0.06$) and the silk treatment was not distinct from the black fly treatment ($A = 0.01$, $P = 0.21$). Additionally, the control channels exhibited significantly higher variation in community composition (i.e. multivariate dispersion; $F = 3.837$, d.f. = 2, $P = 0.04$) than the black fly or silk treatment communities (mean distances to centroid = 0.382, 0.254 and 0.283 for the control, black fly and silk treatments, respectively), as illustrated in the non-metric multidimensional scaling plot (Fig. 3; stress: 0.11, $P = 0.004$, final instability < 0.0001 , $R^2 = 0.904$). The black fly and silk treatments were characterised by higher densities of the mayflies *Dipheter* and *Baetis* (Baetidae) and the midges *Parametricnemus* and *Polypedilum* (Chironomidae). Many of the control replicates had more of the midges *Potthastia gaedii* and *Thienemanniella fusca* and fewer *Ceratopsyche* (Trichoptera: Hydropsychidae) than the black fly and silk replicates (Fig. 3).

We identified a total of 49 taxa from the experimental channels. The three most abundant taxa (all classified as collector-gatherers) were *Baetis tricaudatus*, *Dipheter hageni* and *Thienemanniella xena* (Table 3). Invertebrates

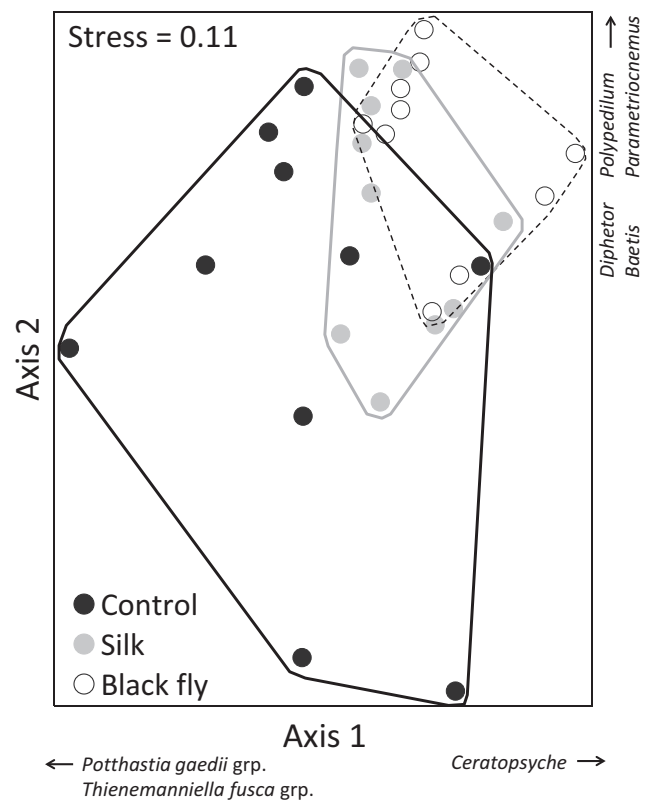


Fig. 3 Non-metric multidimensional ordination plot of all samples from the experiment. The polygons illustrate the range of community composition exhibited by the control (solid black line), silk (solid grey line) and black fly (dashed black line) treatments. The two-dimensional ordination accounted for 90% of the variation in the original species matrix. Influential taxa whose abundances were positively or negatively correlated with ordination axes (Pearson's $|r| \geq 0.5$) are listed for both axes.

classified as predators comprised 2.7, 2.1 and 3.4% of the invertebrates in the black fly, silk and control treatments, respectively, and 5.4% of the benthic samples. Of the 12 most abundant taxa (taxa with grand mean densities ≥ 0.5 invertebrates channel⁻¹, excluding *Simulium*), the lowest mean density was in the control treatment in every case (Table 3). Of these 12 taxa, the highest densities were in the black fly treatment (six taxa) or the silk treatment (five taxa), while the last taxon (the chironomid *Parametricnemus*) was equally abundant in the black fly and silk treatments (Table 3). The rankings of the remaining 37 taxa among treatments were more mixed: 18 were most abundant (or density was equal to other treatments) in the black fly treatment and 14 taxa were most abundant (or equal to other treatments) in both the silk and control treatments. In the control treatment, invertebrate density and richness reached 21.1 and 25.9%, respectively, of that observed in Convict Creek. Thus, the increase in abundance caused by black flies

Table 3 Mean abundances per 0.12 m² of the 12 most common taxa and their functional feeding groups found in our experiment. 0.12 m² is the area of channel used in our experiment ($n = 10$) and the area of Convict Creek that we sampled ($n = 6$). Functional feeding groups (FFG) are from Merritt *et al.* (2008)

Order (or above)	Family	Taxon	FFG	Black			Convict Crk
				fly	Silk	Control	
Ephemeroptera	Baetidae	<i>Baetis tricaudatus</i>	Collector-gatherer	37.8	26.4	14.2	47.3
Ephemeroptera	Baetidae	<i>Dipheter hageni</i>	Collector-gatherer	19.7	15.7	10	41.3
Diptera	Chironomidae	<i>Thienemanniella xena</i>	Collector-gatherer	3.6	4.6	2.9	0.0
Trichoptera	Hydropsychidae	<i>Ceratopsyche</i>	Collector-filterer	2.8	4.1	1.9	4.0
Diptera	Chironomidae	<i>Polypedilum aviceps</i>	Omnivore	1.9	1.8	1.2	13.0
Ephemeroptera	Heptageniidae	<i>Epeorus</i>	Scraper	1.6	1.8	1.2	6.7
Diptera	Chironomidae	<i>Cricotopus/Orthocladius</i>	Collector-gatherer	1.7	1.3	1.1	4.7
Collembola	Collembola	Collembola	Collector-gatherer	1.2	1.5	0.6	0.0
Diptera	Chironomidae	<i>Parametriocnemus</i>	Collector-gatherer	1.0	1.0	0.7	7.3
Oligochaeta	Oligochaeta	Oligochaeta	Collector-gatherer	1.1	0.8	0.7	91.3
Diptera	Chironomidae	<i>Eukiefferiella claripennis</i>	Omnivore	0.8	0.7	0.2	0.3
Coleoptera	Elmidae	<i>Optioservus</i>	Scraper	0.5	0.8	0.1	33.0

and silk occurred mainly among the most numerous taxa (Table 3) and, while our study was necessarily limited in temporal scale, it still allowed for a substantial proportion of invertebrate community recovery.

Discussion

Black fly larvae, acting as ecosystem engineers, increased the resources available to other taxa, thus exerting a net facilitative effect on invertebrate colonisation of newly submerged substrata. Black flies rapidly colonised the control channels, even though they were scarce in the surrounding stream. This is consistent with natural patterns of recovery, as black flies are often among the first colonists in streams recovering from drying (e.g. Bogan *et al.*, 2013). However, *Simulium* is not simply a pioneer, as raised black fly density increased the quantity of algae and detritus, and the density and richness of invertebrates on newly submerged substrata. Because benthic density and diversity normally increase through time following disturbance in streams (e.g. Fisher *et al.*, 1982; Doeg *et al.*, 2006), black flies apparently accelerated community recovery in our study. The similarity in results between the black fly and silk treatments suggests that black flies acted as ecosystem engineers (Jones *et al.*, 1997), as the positive effects of black flies on community recovery were achieved primarily via the silk they secreted. This study is not the first to suggest that black flies are ecosystem engineers; black flies can also affect basal resources by processing smaller organic particles into larger ones through filter feeding and egestion (Wotton *et al.*, 1998). Our study is the first, however, to demonstrate that black flies and their silk may facilitate community recovery following disturbances.

Although black flies can displace some benthic taxa through competitive interactions (Dudley *et al.*, 1990), we found that invertebrate abundance was higher in the black fly treatment than in the silk treatment. This indicates that any negative effects of interspecific competition between black flies and other invertebrates did not override the positive effects of black fly silk on colonists. Invertebrate abundance could have increased in channels with elevated silk because it improved invertebrate 'footing' on substrata, or perhaps invertebrates were attracted to the silk itself. However, our interpretation is that black flies encouraged colonisation by other taxa by increasing the retention of basal resources on disturbed substrata with their silk. Increased algal resources, in particular, have long been associated with higher colonisation rates of benthic taxa (e.g. McAuliffe, 1984). For example, Richards & Minshall (1988) demonstrated that substratum patches with more algae were subject to higher rates of colonisation by the mayfly *Baetis*, one of the dominant genera in our study. Detritus is also essential to stream metabolism and stream food webs (Anderson & Sedell, 1979; Tank *et al.*, 2010), and reductions in detritus can limit the production and growth of many benthic species (e.g. Eggert & Wallace, 2003).

While black flies can be very abundant in the early stages of recovery following disturbance, they may subsequently be displaced by slower-colonising species (Hemphill & Cooper, 1983; Hemphill, 1988). Our study stream, Convict Creek, had not experienced a significant disturbance in the prior 3 months (B. Hammock & M. Bogan, pers. observ.), whereas our experimental channels simulated the first day of recovery from drying disturbance. The relative abundance of black flies in the control channels (which received no added black flies)

was 19 times higher than in the Convict Creek benthos, whereas the relative abundance of invertebrate predators in our experiment was approximately half that of the benthic samples. This suggests that while black flies can dominate recently submerged substrata within a matter of hours, most individuals are eventually displaced, consumed or outcompeted by slower-colonising predators or competitors (e.g. Tikkanen *et al.*, 1997). Ironically, the dominance of black flies on recently disturbed substrata may be so fleeting in part because they improve conditions for their natural enemies.

The significant effect of black flies and silk on the number of colonists also scaled up to community differences among treatments (Fig. 3). If a specific subset of the invertebrate community was more attracted to the increased resources in the black fly and silk treatments than to the control, then we would expect that black fly and silk communities would be similar to each other and perhaps distinct from control communities. This was precisely what we observed and suggests that the ecosystem engineering of black flies exerts deterministic control on the early stages of community recovery on newly submerged substrata. Greater availability of particular resources on silk-covered substrata (e.g. diatoms) may have encouraged rapid colonisation by specialist consumers. In contrast, the control channels could be colonised by generalist feeders that were able to exploit the sparse but diverse food sources, possibly producing the more variable community observed. While both stochastic and deterministic controls are important in stream community assembly (Thompson & Townsend, 2006), black flies may alter the relative importance of these processes, at least over the limited temporal and spatial scales examined in our study.

In perennial streams, the most important pathway by which organisms recolonise the substratum following disturbance is thought to be via drift (Lake, 2000). This recolonisation follows a general pattern. Diatoms colonise the substratum relatively quickly (hours to days), while multicellular algae recover more slowly (weeks to months; e.g. Fisher *et al.*, 1982). In parallel, invertebrate abundance, richness and detritus increase through time before reaching asymptotes (e.g. Doeg *et al.*, 2006). Black flies sped up most of these processes following a simulated disturbance (i.e. rewetting of dry substrata from the floodplain) and thus could be considered 'catalysts' of secondary succession, speeding the numerical and compositional recovery of disturbed sites, perhaps by increasing basal resources. Although the effect of silk on detritus quantity was only weakly positive, the

substratum in the black fly treatment was exposed to silk secretion for eight times longer than that in the silk treatment (3.5 h versus 27.5 h), so it is unsurprising that the effect of silk on detritus was stronger in the presence of black flies. While our study focussed on secondary succession (e.g. recovery from drying), primary succession (e.g. colonisation of new habitat created by receding glaciers) proceeds differently. Aquatic insects are thought to colonise these newly created habitats as winged adults, and simuliids have not been identified as pioneer species during primary succession, at least in Alaska (Milner *et al.*, 2011). Thus, our study suggests only that black flies speed community recovery following disturbance (i.e. secondary succession) and did not address primary succession.

While ecosystem engineering is quite common in streams (Moore, 2006), habitat modifications by black flies may be of particular importance due to their early arrival in secondary succession. Their facilitation of later colonists may be akin to nurse plants that ameliorate conditions by moderating temperature or moisture for subsequent colonists (Scarano, 2002) or alder trees that increase soil nutrients after glaciation (Crocker & Major, 1955; Chapin *et al.*, 1994). However, our experiment was conducted at a small temporal (24 h blocks over 1 month) and spatial (small channels in one stream) scale, and the disturbance was simulated. Thus, additional research is needed to test the link between the results of our study and the influence of black flies on natural community recovery.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. Diatoms in black fly silk on a glass slide (magnification = 400×; photo taken by Thomas Smith).

Table S1. Parameter estimates and 95% confidence intervals for the top-ranked chlorophyll *a* ($\mu\text{g channel}^{-1}$) model.

Table S2. Parameter estimates and 95% confidence intervals for the top-ranked detritus (mg channel^{-1}) model.

Table S3. Parameter estimates and 95% confidence intervals for the top-ranked invertebrate density (non-black fly invertebrates channel^{-1}) model.

Table S4. Parameter estimates and 95% confidence intervals for the top-ranked taxon richness (taxa channel^{-1}) model.

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