Organic agriculture promotes evenness and natural pest control

David W. Crowder[1], Tobin D. Northfield[1], Michael R. Strand[2] & William E. Snyder[1]

Human activity can degrade ecosystem function by reducing species number (richness)[1–4] and by skewing the relative abundance of species (evenness)[5–7]. Conservation efforts often focus on restoring or maintaining species number[8,9], reflecting the well-known impacts of richness on many ecological processes[1–4]. In contrast, the ecological effects of disrupted evenness have received far less attention[7], and developing strategies for restoring evenness remains a conceptual challenge[7]. In farmlands, agricultural pest-management practices often lead to altered food web structure and communities dominated by a few common species, which together contribute to pest outbreaks[6,7,10,11]. Here we show that organic farming methods mitigate this ecological damage by promoting evenness among natural enemies. In field enclosures, very even communities of predator and pathogen biological control agents, typical of organic farms, exerted the strongest pest control and yielded the largest plants. In contrast, pest densities were high and plant biomass was low when enemy evenness was disrupted, as is typical under conventional management. Our results were independent of the numerically dominant predator or pathogen species, and so resulted from evenness itself. Moreover, evenness effects among natural enemy groups were independent and complementary. Our results strengthen the argument that rejuvenation of ecosystem function requires restoration of species evenness, rather than just richness. Organic farming potentially offers a means of returning functional evenness to ecosystems.

Declines in species richness alter ecosystem processes across many communities[1–4]. Interventions that preserve rare species, or restore extirpated species, are widely deployed to mitigate species loss[8,9]. Such efforts are relatively straightforward because they can be targeted to the needs of particular rare species. In contrast, little is known about how disparities in species abundance degrade ecosystem function, or what management practices might mitigate this damage by restoring community evenness[7]. This is unfortunate because human-induced environmental degradation can skew the relative commonness of species[7], and because uneven communities are often more susceptible to invasion[12] and less resilient to disturbance[13].

Biological pest control is a valuable ecosystem service[14–16], but intensification of farming can drastically distort the relative-abundance distributions of natural enemy communities in favour of a few dominant species[5–7,10,11]. We investigated whether organic farming might, by increasing diversity among natural enemies, improve natural control of the pestiferous potato beetle *Leptinotarsa decemlineata* in potato (*Solanum tuberosum*). Predatory bugs (primarily *Nabis alternatus* and *Geocoris bullatus*) and beetles (primarily *Hippodamia convergens* and *Pterostichus melanarius*) attack *L. decemlineata* in foliage where it feeds[17], and pathogenic nematodes and fungi (represented by the nematodes *Heterorhabditis megidis* and *Steinernema carpocapsae* and the fungus *Beauveria bassiana*) occur below ground and attack the herbivore in the soil where it pupates[18,19].

We first investigated whether organic farming affects either of the two components of natural enemy biodiversity, richness and evenness, by analysing data from surveys of predators and pathogens in Washington potato fields[17,18]. We found no impact of pest-management regime on natural enemy richness (Supplementary Fig. 1), but evenness of natural enemies drastically differed between organic and conventional potato fields (Fig. 1). Higher evenness in organic fields reflected relatively equitable distributions of natural enemies, whereas conventional fields were relatively uneven because they were numerically dominated by one enemy taxon (Fig. 2). Indeed, just one species accounted for up to 80% of individuals in conventional fields, whereas the most abundant species in organic fields comprised as little as 38% of the predator or pathogen community (Fig. 2). To examine whether organic management generally promotes greater enemy evenness, rather than being a feature unique to our potato fields, we surveyed the literature for studies that reported the abundances of at least three taxonomic groups of natural enemies in organic and conventional fields of the same crop. We found 38 such
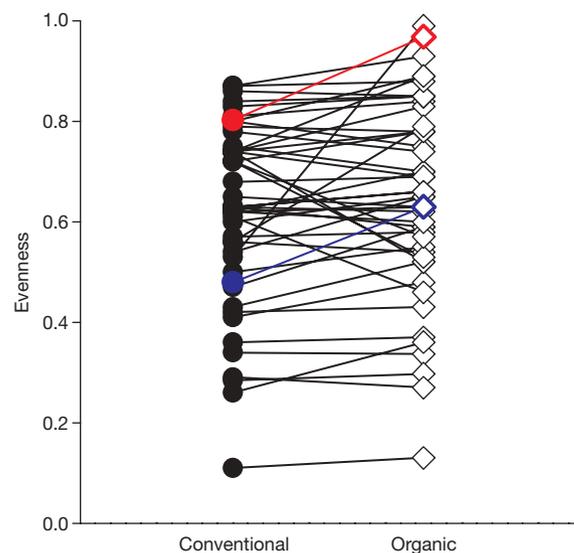

Figure 1 | Evenness of natural enemies across cropping systems. Lines connect evenness values in conventional (circles)/organic (diamonds) pairs from each comparison in the meta-analysis. In the overall meta-analysis, natural enemy evenness was significantly greater in organic than in conventional fields (median 7.2% increase: $SR_+ = 177.0$ (signed-rank test statistic), $N = 48$, $P = 0.044$). Similarly, predator evenness in Washington potato fields (blue symbols and line) was significantly greater in organic than in conventional fields ($t = 2.28$, d.f. = 18, $P = 0.035$); pathogen evenness (red symbols and line) was also greater in organic potato fields, although this difference was not significant ($N = 19$, $P = 0.19$).

[1]Department of Entomology, Washington State University, Pullman, Washington 99164, USA. [2]Department of Entomology, University of Georgia, Athens, Georgia 30602, USA.
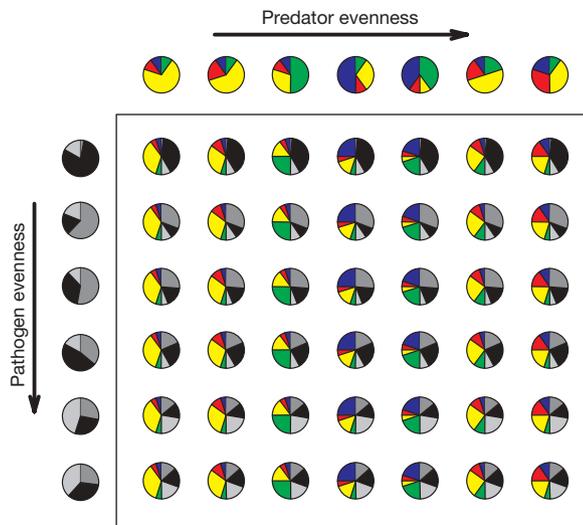
Figure 2 | Predator and pathogen evenness in the field-enclosure experiment. The top row shows the seven levels of predator evenness included in the field-enclosure experiment (Supplementary Table 2), and the leftmost column presents the six levels of pathogen evenness (Supplementary Table 2) that were included. These were fully crossed to yield 42 unique predator–pathogen evenness compositions (shown in the box). Predators were *G. bullatus* (yellow), *N. alternatus* (green), *H. convergens* (red) and *P. melanarius* (blue). Pathogens were *H. megidis* (black), *S. carpocapsae* (dark grey) and *B. bassiana* (light grey).

studies, which provided 40 predator and 8 insect pathogen comparisons spanning 23 crops in 16 countries (Supplementary Table 1). Notably, this meta-analysis revealed significantly greater evenness in organic fields than in conventionally managed fields (Fig. 1).

On the basis of these field surveys, we assessed whether differences in natural enemy evenness observed in potato fields affected pest suppression. We approached this by experimentally manipulating predator and pathogen evenness in field enclosures and recording the resultant effects on plant growth and potato beetle mortality. Our predator and pathogen evenness treatments reproduced relative-abundance ratios from our potato field surveys[17,18], and so reflected the natural range of variation across organic and conventional fields (Fig. 2 and Supplementary Fig. 2). Because fields vary in which natural enemy species dominates, our evenness treatments also differed in the identity of the most abundant enemy species (Fig. 2 and Supplementary Table 2). The field survey data provided seven different real-world predator evenness distributions and six different pathogen evenness distributions, which we crossed within a fully factorial design to obtain 42 unique predator–pathogen evenness combinations (Fig. 2). By separately manipulating evenness among predators and among pathogens in the same experiment, we could evaluate whether evenness effects among these two enemy classes were independent and complementary. Total predator and pathogen densities were held constant across our evenness treatments within a substitutive design to avoid confounding effects of enemy density. In our field surveys, all common enemy species were recovered from nearly all fields, with omissions probably resulting from sampling intensity rather than true absence; all treatments therefore received all natural enemy species (that is, richness was constant). Our experiment spanned >1 herbivore generation, such that all herbivores encountered both foliar predators and soil-dwelling pathogens.

Increasing natural enemy evenness in our field enclosures triggered a powerful trophic cascade beneficial to plants and harmful to herbivores. Evenness among predators and pathogens acted independently to increase plant biomass (predator evenness slope: 0.49 [0.15, 0.82] (throughout, square brackets indicate the 95% confidence interval), $t = 2.96$, d.f. = 39, $P = 0.0052$; pathogen evenness slope: 0.32 [0.16, 0.48], $t = 4.01$, d.f. = 39, $P = 0.0003$; predator–pathogen interaction:

$P > 0.15$; Fig. 3a and Supplementary Fig. 3), such that the largest plants occurred in treatments where both predators and pathogens were evenly distributed. Importantly, above-ground biomass strongly correlates with potato tuber yield[20], suggesting that natural enemy evenness increases yield. Consistent with this effect on plants, greater natural enemy evenness increased potato beetle mortality, with effects of predator and pathogen evenness again being fully additive and complementary (predator evenness slope: -0.96 [-1.68, -0.22], $t = -2.92$, d.f. = 39, $P = 0.0058$; pathogen evenness slope: -0.40 [-0.75, -0.046], $t = -2.55$, d.f. = 39, $P = 0.015$; predator–pathogen interaction: $P > 0.15$; Fig. 3b and Supplementary Fig. 3). Evenness effects were independent of any natural enemy species being numerically dominant, as the abundance of each enemy species was neither retained in stepwise regression models (Supplementary Tables 3 and
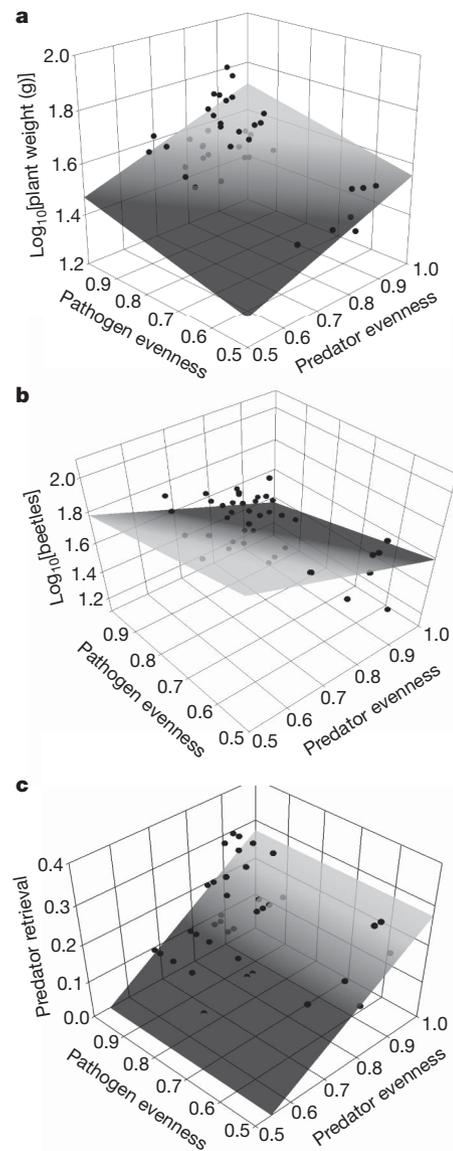

Figure 3 | Effects of natural enemy evenness on multiple trophic levels. Cascading effects of predator and pathogen evenness on final plant weight (log$_{10}$ transformed; **a**), final densities of herbivorous potato beetles (log$_{10}$ transformed; **b**) and final predator retrieval (ratio of number recovered to number released; **c**). In each panel, the response of each of the 42 experimental arenas is indicated with a circle, and the plane indicates the two-dimensional trend in the data. The shading of the plane darkens as the response values decrease along either evenness axis and lightens as the response values increase.

4) nor significant in models selected using information criteria (Supplementary Tables 5–7). These results suggest that greater community evenness, rather than the impact of any single enemy species, underlies cascading effects on herbivores and plants. Our field enclosures simplified the overall prey community by excluding non-pest prey. However, organic and conventional potato fields in our region did not differ in the abundance or richness of non-pest prey (Supplementary Fig. 4), suggesting that the absence of alternative prey would not bias overall predation rates in favour of one pest-management regime over the other.

As for consumers at other trophic levels, the effects of natural enemy diversity could be transmitted through changes either in per capita resource (prey) consumption or consumer density[4]. Predation among natural enemy species (that is, intraguild predation) also sometimes determines predator richness-function relationships[21–23]. For the community of natural enemies attacking potato beetles, intraguild predation could result from pathogens killing predators or predators killing one another (pathogens do not kill one another, and predators do not attack pathogens). Our results showed that predator survival increased with predator evenness (predator evenness slope: 0.57 [0.29, 0.85], $t = 4.10$, d.f. = 40, $P = 0.0002$; Fig. 3c), indicating that predators benefited from being among competitors that are more heterospecific than conspecific. In contrast, predator survival was unaffected by pathogen evenness (Fig. 3c and Supplementary Tables 3 and 7), which probably reflects their spatial separation[23]. The above-ground predators attack only eggs and early-stage herbivore larvae, and these prey stages were primarily available to predators only in the first week of the experiment[19]. Thus, benefits of initial predator evenness for predator survival probably reflected greater per capita foraging success when prey were abundant, and/or reduced predator interference, leading to greater ability to withstand an extended period of starvation.

As previously noted, our meta-analysis shows that natural enemy communities are significantly more even in organic than in conventional agroecosystems (Fig. 1). These findings raise the question of whether the benefits of greater natural enemy evenness for natural pest control are also a general feature of organic farming. Unfortunately, with a few exceptions[10,11,24], survey comparisons of organic and conventional fields rarely include a measure of predation/disease pressure on pests. In our potato system, the evenness increase between conventional and organic farms (Fig. 1) translates into pest densities 18% lower and plants 35% larger (Fig. 3), suggesting that benefits of evenness for pest control may somewhat offset yield losses to reduced insecticide use. It may be that greater evenness and other enemy-diversity benefits of organic production[25,26] contribute to organic farmers' ability to reduce insecticide use while maintaining pest densities similar to conventional farms[25]. Our results, however, are based on field-enclosure experiments, which allow careful manipulation of natural enemy community composition but block longer-range insect movement and reduce prey diversity. Thus, further studies comparing pest-control intensity and effects of natural enemy evenness in organic and conventional fields are strongly warranted, ideally outside field enclosures when possible.

Evidence is rapidly accumulating that species evenness, which has been neglected relative to species richness, has a similarly broad range of ecological impacts[7]. Thus, both the number and relative abundances of species must be sustained to achieve vigorous ecosystem functioning. Attempts to maintain or restore evenness will be particularly challenging, because strategies must be developed that affect the commonness of many species across communities. Our results suggest that organic agriculture presents one management solution that meets this challenge. The specific mechanism through which organic agriculture fosters greater enemy evenness remains unclear, but reduced use of broad-spectrum pesticides could be one factor given that non-selective pesticides kill many species[24–26]. Although ecologists have just begun to examine the mechanisms underlying evenness effects, work so far suggests that many of the processes

underlying the impacts of species richness may be at work[7]. For example, evenness among bacteria promotes resilience to disturbance by ensuring sufficient densities of species in key functional roles[13], analogous to the 'insurance effect' in the species richness literature[27,28]. Similarly, our study shows that natural pest control is improved by the additive effects of evenness in two ecologically distinct consumer groups, predators and pathogens, similar to the niche complementarity that commonly underlies species richness effects[29,30]. One possibility is that evenness and richness effects fall along a continuum, with declining evenness leading to increasingly underused niches that become fully vacant once species are lost. Our study highlights the important role of evenness in ecosystems and provides evidence that the restoration of functional evenness through habitat management, although conceptually daunting, is an achievable goal.

METHODS SUMMARY

Field and literature surveys. Predator and pathogen evenness scores for Washington potato fields were extracted from published surveys[17,18], calculated using Shannon's evenness index and compared using two sample t-tests (predators) or nonparametric permutation tests (pathogens). We calculated evenness scores for paired predator and pathogen comparisons from our literature search using Shannon's index, and compared these scores using Wilcoxon signed-rank tests.

Field-enclosure experiment. The relative proportions of natural enemies in evenness treatments (Fig. 2 and Supplementary Table 2) were derived from representative potato fields (Supplementary Fig. 2), such that enemy relative abundances reproduced real-world values[17,18]. Specific treatments were selected to maximize the range of evenness values for each guild, while ensuring that the dominant species varied among treatments. Total densities of ten predators per arena were established in all replicates within our substitutive design, reflecting typical field densities[17,19]. For each evenness composition, we determined the number of individuals of each species to be released by multiplying the proportional abundance of that species in the field that served as that composition's model by the total number of predators released (ten), rounded to the nearest whole number and such that at least one individual per species was released into each replicate to maintain constant richness (Fig. 2 and Supplementary Table 2). The same process was used to determine pathogen densities based on estimated typical densities of each taxon in surveyed fields (2.5×10^4 nematodes per square metre or 10^9 fungal spores per square metre)[18,19]. Field enclosures were plastic tubs buried in the soil and covered by mesh cages, located in an agricultural field in Pullman, Washington. We transplanted potatoes into each enclosure and later released potato beetle eggs and larvae, pathogens and predators. After 31 days (potato beetle development from egg to adult takes about 28 days), we counted the number of herbivores and predators in enclosures, and harvested and dried plants.

Full Methods and any associated references are available in the online version of the paper at www.nature.com/nature.

1. Chapin, F. S. *et al.* Biotic control over the functioning of ecosystems. *Science* **277**, 500–504 (1997).
2. Loreau, M. *et al.* Biodiversity and ecosystem functioning: current knowledge and future challenges. *Science* **294**, 804–808 (2001).
3. Hooper, D. U. *et al.* Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecol. Monogr.* **75**, 3–35 (2005).
4. Cardinale, B. J. *et al.* Effects of biodiversity on the functioning of trophic groups and ecosystems. *Nature* **443**, 989–992 (2006).
5. Chapin, F. S. III *et al.* Consequences of changing biodiversity. *Nature* **405**, 234–242 (2000).
6. Matson, P. A., Parton, W. J., Power, A. G. & Swift, M. J. Agricultural intensification and ecosystem properties. *Science* **277**, 504–509 (1997).
7. Hillebrand, H., Bennett, D. M. & Cadotte, M. W. Consequences of dominance: a review of evenness effects on local and regional ecosystem processes. *Ecology* **89**, 1510–1520 (2008).
8. Srivastava, D. S. & Vellend, M. Biodiversity-ecosystem function research: is it relevant to conservation? *Annu. Rev. Ecol. Evol. Syst.* **36**, 267–294 (2005).
9. Benayas, J. M. R., Newton, A. C., Diaz, A. & Bullock, J. M. Enhancement of biodiversity and ecosystem services by ecological restoration: a meta-analysis. *Science* **325**, 1121–1124 (2009).
10. Tylianakis, J. M., Tscharntke, T. & Lewis, O. T. Habitat modification alters the structure of tropical host–parasitoid food webs. *Nature* **445**, 202–205 (2007).
11. Macfadyen, S. *et al.* Do differences in food web structure between organic and conventional farms affect the ecosystem service of pest control? *Ecol. Lett.* **12**, 229–238 (2009).

12. Wilsey, B. J. & Polley, H. W. Reductions in grassland species evenness increase dicot seedling invasion and spittle bug infestation. *Ecol. Lett.* **5,** 676–684 (2002).
13. Wittebolle, L. *et al.* Initial community evenness favours functionality under selective stress. *Nature* **458,** 623–626 (2009).
14. Bianchi, F. J. J. A., Booij, C. J. H. & Tscharntke, T. Sustainable pest regulation in agricultural landscapes: a review on landscape composition, biodiversity, and natural pest control. *Proc. R. Soc. B* **273,** 1715–1727 (2006).
15. Losey, J. E. & Vaughan, M. The economic value of ecological services provided by insects. *Bioscience* **56,** 311–323 (2006).
16. Landis, D. A., Gardiner, M. M., van der Werf, W. & Swinton, S. M. Increasing corn for biofuel production reduces biocontrol services in agricultural landscapes. *Proc. Natl Acad. Sci. USA* **105,** 20552–20557 (2008).
17. Koss, A. M., Jensen, A. S., Schreiber, A., Pike, K. S. & Snyder, W. E. A comparison of predator and pest communities in Washington potato fields treated with broad-spectrum, selective or organic insecticides. *Environ. Entomol.* **34,** 87–95 (2005).
18. Ramirez, R. A., Henderson, D. R., Riga, E., Lacey, L. A. & Snyder, W. E. Harmful effects of mustard bio-fumigants on entomopathogenic nematodes. *Biol. Control* **48,** 147–154 (2009).
19. Ramirez, R. A. & Snyder, W. E. Scared sick? Predator-pathogen facilitation enhances exploitation of a shared resource. *Ecology* **90,** 2832–2839 (2009).
20. Donnelly, A., Craigon, J., Black, C. R., Colls, J. J. & Landon, G. Elevated CO_2 increases biomass and tuber yield in potato even at high ozone concentrations. *New Phytol.* **149,** 265–274 (2001).
21. Finke, D. L. & Denno, R. F. Predator diversity dampens trophic cascades. *Nature* **429,** 407–410 (2004).
22. Casula, P., Wilby, A. & Thomas, M. B. Understanding biodiversity effects on prey in multi-enemy systems. *Ecol. Lett.* **9,** 995–1004 (2006).
23. Schmitz, O. J. Predator diversity and trophic interactions. *Ecology* **88,** 2415–2426 (2007).
24. Letourneau, D. B. & Bothwell, S. G. Comparison of organic and conventional farms: challenging ecologists to make biodiversity functional. *Front. Ecol. Environ* **6,** 430–438 (2008).
25. Bengtsson, J., Ahnström, J. & Weibull, A.-C. The effects of organic agriculture on biodiversity and abundance: a meta-analysis. *J. Appl. Ecol.* **42,** 261–269 (2005).
26. Hole, D. G. *et al.* Does organic farming benefit biodiversity? *Biol. Conserv.* **122,** 113–130 (2005).
27. Gitay, H., Wilson, J. B. & Lee, W. G. Species redundancy: a redundant concept? *J. Ecol.* **84,** 121–124 (1996).
28. Yachi, S. & Loreau, M. Biodiversity and ecosystem productivity in a fluctuating environment: the insurance hypothesis. *Proc. Natl Acad. Sci. USA* **96,** 1463–1468 (1999).
29. Silvertown, J., Dodd, M. E., Gowing, D. J. D. & Mountford, J. O. Hydrologically defined niches reveal a basis for species richness in plant communities. *Nature* **400,** 61–63 (1999).
30. Finke, D. L. & Snyder, W. E. Niche partitioning increases resource exploitation by diverse communities. *Science* **321,** 1488–1490 (2008).

METHODS

Predator and pathogen evenness in Washington potato fields. Details of the natural enemy field censuses are included in refs 17, 18. Briefly, the surveys encompassed organic and conventional fields of similar size, often managed by the same grower, and fully interspersed throughout the irrigated agricultural region of central Washington. Because most farms included both organic and conventional fields at the same site, landscape context did not differ in any systematic way between organic and conventional fields[17,18]. Pest-management regimes were verified using grower spray records. Foliar pests in organic fields were treated with infrequent sprays of natural product pesticides, and soil pests were managed using mustard cover crops planted the autumn preceding the potato planting (mustard breakdown products act as soil fumigants). Conventional fields were treated with frequent applications of broad-spectrum foliar pesticides and soil fumigants. Predators were vacuum-collected from plant foliage[17], and pathogens were collected using sentinel waxworm (*Galleria mellonella*) larvae buried in the soil[18]. The predator survey included 12 conventional and 8 organic fields. The pathogen survey included 17 conventional and 2 organic fields. From each study, we calculated natural enemy evenness using Shannon's index, $J = H'/H_{max}$, where $H' = \sum_{i=1}^{S} (-p_i \ln p_i)$, $H_{max} = \ln S$, p_i is the proportion of individuals in taxonomic group i and S is the total number of taxonomic groups (that is, richness). Values for J range from 0 to 1, with 0 representing entirely skewed dominance by one group and 1 representing perfectly even relative abundances among groups. We also calculated richness based on the number of predator families or pathogen genera. Values for evenness and richness were compared using two sample *t*-tests (predators) or nonparametric permutation tests (pathogens; parametric tests were not appropriate for pathogens owing to low replicate number).

Diversity in conventional versus organic agriculture. We started our search using the reference lists of two reviews[25,26], and supplemented these by searching the ISI Web of Knowledge using the terms 'conventional' and 'organic' and refining the criteria to include the categories 'agriculture, multidisciplinary', 'biodiversity and conservation', 'biology', 'ecology', 'entomology', 'environmental sciences' and 'zoology'. Data from each paper were obtained from figures or tables or from authors. Using these data, we calculated evenness in fields of each type, for each study, using Shannon's index. If a study measured abundance at multiple times, the average value was used. These values were used to calculate the log-response ratio[31]. The log-response ratio was not normally distributed (Shapiro–Wilk test: $P = 0.013$), so Wilcoxon signed-rank tests were used to compare across field types.

Field-enclosure experiment. Our field experiment included representatives of the four dominant families of potato beetle predators in the field surveys (Carabidae, Coccinellidae, Geocoridae and Nabidae, represented in the experiment by the dominant species *P. melanarius*, *H. convergens*, *G. bullatus* and *N. alternatus*, respectively), which together made up >95% of all potato beetle predators collected[17]. All three insect pathogen genera recovered in the below-ground-enemy survey (*Heterorhabditis*, *Steinernema* and *Beauveria*) were represented in the experiment by the nematodes *H. megidis* and *S. carpocapsae* and the fungus *B. bassiana*[18]. Our experiment fully crossed seven levels of predator evenness with six levels of pathogen evenness, each replicated once for a total of 42 replicates (Fig. 2 and Supplementary Table 2).

The field-enclosure experiment was conducted in an agricultural field at the Tukey Experimental Orchard, located on the campus of Washington State University in Pullman, Washington. The base of each experimental unit consisted of a 68-l plastic tub (0.6 m × 0.4 m × 0.4 m), buried flush with the ground and filled with soil from the surrounding field. Entomopathogens are naturally rare in this soil[19]. Each tub was covered above ground with a PVC frame (0.6 m × 0.5 m × 0.3 m) covered with mesh fabric, with a zipper to allow access. Thus, enclosures contained both below-ground and above-ground natural enemy communities[19]. Into each cage we transplanted two six-week-old potato plants that had been started in a greenhouse (25 °C, 50% RH, ambient light). We then added five clutches of 20 potato beetle eggs, and 20 each of first–second- and third–fourth-instar larvae, collected from a potato field in Othello, Washington. This density is well within the range of open-field values[17]. We allowed 24 h for potato beetles to establish feeding positions, and then released predators and pathogens. Predators were field-collected within 3 d of the initiation of the experiments, by hand or using pitfall traps. Nematodes were provided by Becker Underwood and *B. bassiana* were provided by Bioworks (Mycotrol-O). The pathogens were applied using a spray bottle to coat the soil evenly[19].

Pathogen application reproduced typical infection rates in the field survey[18,19]. There were also six replicates of a no-enemy control. At the end of the experiment, each cage was hand-searched for 15 min to collect predators, adult potato beetles (all potato beetles initially added were adults by this time) and potato beetle larvae (representing the F_1 generation produced *in situ* over the last few days of the experiment). Potato beetles initially added to enclosures were in stages vulnerable to predation during the first week of the experiment[19], and so predators experienced low-prey conditions for ~3 weeks by the end of the experiment, resulting in low final predator densities (Fig. 3c). However, in similar experiments enemy recovery after 7 d was ~85% (ref. 19), suggesting that vulnerable potato beetle stages were exposed to predator communities that closely resembled those initially established. Finally, all above-ground plant material was harvested, dried for 3 d at 100 °C and weighed.

To verify that our enemies affected herbivores and plants, we compared final plant weight and potato beetle densities across the enemy addition treatments to that in the controls (using two-sample *t*-tests; Supplementary Fig. 5). To determine whether these impacts depended on the evenness of natural enemy communities, or the identity of constituent species, we used stepwise regression to determine whether plant weight, potato beetle density and predator retrieval were affected by the explanatory variables predator evenness, pathogen evenness, predator–pathogen interaction and the abundance of each enemy species. Stepwise regression was used for model selection because multi-collinearity among some of the explanatory variables would have violated assumptions of multiple regression if the complete model with all ten explanatory variables had been used[32]. We used both forward and backward stepwise regression to determine whether model selection procedures affected results. In each forward step, we added the explanatory variable with the highest *t*-statistic, and in each backward step we removed the explanatory variable with the lowest *t*-statistic[32]. We used a conservative criterion for these steps ($\alpha = 0.15$) to ensure that any variables not retained in stepwise regression models would not significantly affect parameter estimation. After models were selected, we performed extra sum-of-squares *F*-tests[32] to determine whether the reduced model (with fewer variables) fit the data worse than the full model with all predictors, where a lack of significant effects in extra sum-of-squares *F*-tests indicated that the dropped parameters did not improve the fit of the model. For both stepwise regression and information criterion approaches (see below), we ensured that all models including the predator–pathogen interaction term also had both main effects (predator evenness and pathogen evenness). Forward and backward stepwise regression produced the same models with each response (Supplementary Table 3), indicating that model selection procedures did not affect the results.

To verify that models selected using stepwise regression produced an optimal fit to the observed data, we used information criteria[32,33] to examine the fit of all possible models for each response (plant weight, potato beetle density and predator retrieval). For each response, there were 1,023 possible models, each representing a unique combination of the ten explanatory variables. For each model, we calculated the Akaike information criterion and the Schwarz-Bayesian information criterion, which are commonly used information criteria for model selection[32,33]. Each of these criteria rewards models that have a better fit to the observed data and penalizes models with large numbers of insignificant predictors[32]. For each criterion, lower values indicate a more parsimonious model. The most parsimonious models identified using information criteria (Supplementary Tables 5–7) were always the same as those selected using stepwise regression (Supplementary Tables 3 and 4). Additionally, the variables retained from stepwise regression were the only significant variables in each of the 20 most parsimonious models selected using information criteria for each response (Supplementary Tables 5–7). This strongly indicated that inclusion of variables other than those selected during stepwise regression did not affect the results. As the models selected using stepwise regression and information criteria were the same, these models were used for all further analyses after the models were analysed to ensure they met assumptions of normality and homogeneity of variance (Supplementary Table 8).

31. Hedges, L. V., Gurevitch, J. & Curtis, P. S. The meta-analysis of response ratios in experimental ecology. *Ecology* **80**, 1150–1156 (1999).
32. Kutner, M. H., Nachtsheim, C. J., Neter, J., &. Li, W. *Applied Linear Statistical Models* (McGraw-Hill/Irwin, 2005).
33. Whittingham, M. J., Stephens, P. A., Bradbury, R. B. & Freckleton, R. P. Why do we still use stepwise modeling in ecology and behaviour? *J. Anim. Ecol.* **75**, 1182–1189 (2006).