on the basis of regressions of molar area versus body mass in living primates[29]. The smaller primate from this locality is *Eosimias centennicus*, a basal anthropoid that weighed 90–180 g on the basis of similar regressions[2] (all estimates of body mass for eosimiids provided here are ranges of mean estimates derived from multiple regressions). Regressions of talar dimensions versus body mass in living primates[30] show that IVPP V11846 belonged to a primate weighting 90–147 g. Thus, on the basis of size alone, this talus can be confidently allocated to *Eosimias centennicus*. This allocation permits the recognition of additional *Eosimias* tali ($n = 7$) from the Shanghuang fissures. Estimates of body mass for the Shanghuang sample of *Eosimias* tali range from 57 to 118 g, which overlaps the estimated body mass of *Eosimias sinensis* from Shanghuang on the basis of molar regressions (67–137 g). However, several size classes seem to be represented in the Shanghuang sample of tali, and these probably correspond to more than one eosimiid species. Primate calcanei for Shanghuang ($n = 12$) are referred to *Eosimias* on the basis of their functional congruence with the tali from Shanghuang discussed above, as well as their size, provenance and combination of omomyid-like and anthropoid-like traits.

## Phylogenetic analysis

Eleven tarsal characters were subjected to a parsimony analysis using PAUP 4.0 (ref. 18) yielding the nine most parsimonious trees with a consistency index of 0.696. The strict consensus tree is shown in Fig. 4. In all trees, *Eosimias* groups with "telanthropoids"[5] (in this case, the clade including *Apidium* and *Saimiri*). The 'outgroup' consists of character states known in the most likely outgroups of primates: Scandentia, Dermoptera and Plesiadapiformes; these taxa differ insignificantly in the expression of these traits.

Nodes for telanthropoids, Anthropoidea, Haplorhini and Adapiformes are labelled in Fig. 4; the percentages are bootstrap values from 100 replications. Synapomorphies for Antrhopoidea are the shape of the calcaneocuboid joint and a reduced medial talar facet. Synapomorphies for telanthropoids are an increased talar neck angle, an increased talar width and loss of the posterior trochlear shelf. Synapomorphies for Haplorhini are an increased distal length of the calcaneous, a relatively short heel, a steep sided talofibular facet with a lantar lip and a centrally located flexor fibularis groove. Synapomorphies for Adapiformes are a sloping talofibular facet, an increase in the size of the posterior trochlear shelf, a long and narrow posterior astragalocalcaneal facet, an increase in the size of the talotibial facet and an increase in the height of the talar body.

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# Soil pathogens and spatial patterns of seedling mortality in a temperate tree

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The Janzen–Connell hypothesis[1,2] proposes that host-specific, distance- and/or density-dependent predators and herbivores maintain high tree diversity in tropical forests. Negative feedback between plant and soil communities could be a more effective mechanism promoting species coexistence because soil pathogens can increase rapidly in the presence of their host[3], causing conditions unfavourable for local conspecific recruitment[4–6]. Here we show that a soil pathogen leads to patterns of seedling mortality in a temperate tree (*Prunus serotina*) as predicted by the Janzen–Connell hypothesis. In the field, the mean distance to parent of seedling cohorts shifted away from maternal trees over a period of 3 years. Seedlings were grown in soil collected 0–5 m or 25–30 m from *Prunus* trees. Sterilization of soil collected beneath trees improved seedling survival relative to unsterilized soil, whereas sterilization of distant soil did not affect survival. *Pythium* spp., isolated from roots of dying seedlings and used to inoculate healthy seedlings, decreased survival by 65% relative to controls. Our results provide the most complete evidence that native pathogens influence tree distributions, as predicted by the Janzen–Connell hypothesis, and suggest that similar ecological mechanisms operate in tropical and temperate forests.

Aggregated spatial distributions of tree species are expected when seed dispersal is highest beneath maternal trees and seedling mortality occurs at random. In contrast, the Janzen–Connell hypothesis predicts that natural enemies will reduce offspring density beneath trees, creating opportunities for heterospecific recruitment. Empirical and theoretical tests of the hypothesis have yielded mixed results[7–16]. This inconsistency has been attributed, in some cases, to predator satiation, whereby seeds or seedlings close to conspecific trees occasionally escape attack[17–19]. Escape is less likely with microbial pathogens that exhibit positive density dependence[20]. Recent studies in temperate communities have suggested that plant-soil feedbacks affect successional dynamics and species diversity[3,4,21–25]. In this study, we investigated whether negative plant-soil feedback was occurring in *Prunus serotina* (black cherry). Black cherry is a mid-successional tree that produces large numbers of bird-dispersed fruits throughout temperate forests

of eastern North America. Preliminary studies showed that black cherry seedlings experience high mortality in soil collected beneath conspecific adults, but low mortality in soil collected beneath heterospecific adults.

Demographic censuses were conducted beneath six focal black cherry trees from 1996 to 1998. Seed density was significantly

greater 0–10 m from the parent tree than 10–30 m ($187 \pm 14.6\,m^{-2}$ versus $3.60 \pm 0.11\,m^{-2}$, $P = 0.05$ (means $\pm$ s.e.)). Although most seedlings germinate within 10 m of the tree, these seedlings have the lowest survival probability (Fig. 1a–c). With random mortality, mean distance to parent will not change over time. However, mean distance to parent of most seedling cohorts shifted outward. For example, the 1996 cohort beneath tree 1 shifted from 11.1 m at germination to 14.3 m 16 months later. Similarly, the 1998 cohort beneath tree 4 shifted from 8.6 m at germination to 10.8 m in just 4 months.

The overall pattern found when seedlings beneath all focal trees were combined revealed that mean distance to parent of survivors was significantly greater (as determined by boot strapped 95% confidence interval, data not shown) than that of germinating seedlings for 1996 (12.4 m versus 14.8 m), 1997 (8.3 m versus 10.0 m) and 1998 (11.0 m compared with 13.4 m) cohorts. There were also pronounced outward shifts between initial and final censuses of saplings established before the study (tree 1, 16.3 m to 16.8 m; tree 4, 12.3 m to 13.2 m; tree 5, 12.2 m to 13.2 m; tree 6, 14.9 m to 16.3 m). Notably, there were no saplings taller than 2 m or with a basal diameter greater than 3 cm in any of the six study arcs, despite high seedling densities. Continued distance-dependent mortality of older individuals could result from current effects of pathogens on sapling root systems or from residual effects of earlier damage.

The change in mean distance to parent differed among trees. Cohorts beneath trees 2 and 3 exhibited a small decrease in mean distance to parent between germination and the final census date, whereas the mean of cohorts beneath trees 1, 4, 5 and 6 increased ($-0.93 \pm 0.44$ m (1 outlier excluded) versus 1.2 $\pm$ 0.44 m, $P = 0.01$). Shifts in distance appear to be correlated with cohort size (trees 2 and 3, $31.8 \pm 7.2$ seedlings per cohort versus trees 1, 4, 5 and 6, $165.1 \pm 51.8$ seedlings per cohort, $P = 0.04$). Janzen[1] suggested that trees with small seed crops might have less influence on local seed predators than more productive trees further away. Tree diameter at breast height (trees 2 and 3, $36.8 \pm 8.7$ cm, versus trees 1, 4, 5 and 6, $47.6 \pm 7.4$ cm, $P = 0.23$) might also be important, although small sample sizes limit statistical power. If tree diameter is correlated with root system size, then smaller trees will have a weaker influence on conspecific seedlings. Finally, both tree and cohort sizes are often related to tree age. With negative feedback, individuals 'culture' (*sensu lato*)[25] their soil communities leading to a positive correlation between pathogen accumulation and time that a site has been occupied by a species. Seedlings beneath larger and more fecund trees would therefore experience greater distance- and/or density-dependent mortality.

Increased mortality close to the adult could be due to distance- and/or density-responsive factors. Distance and density are negatively correlated because higher densities occur closer to the tree. We used logistic regression analyses to separate these effects. Data from all cohorts were combined to create one model. Both distance to
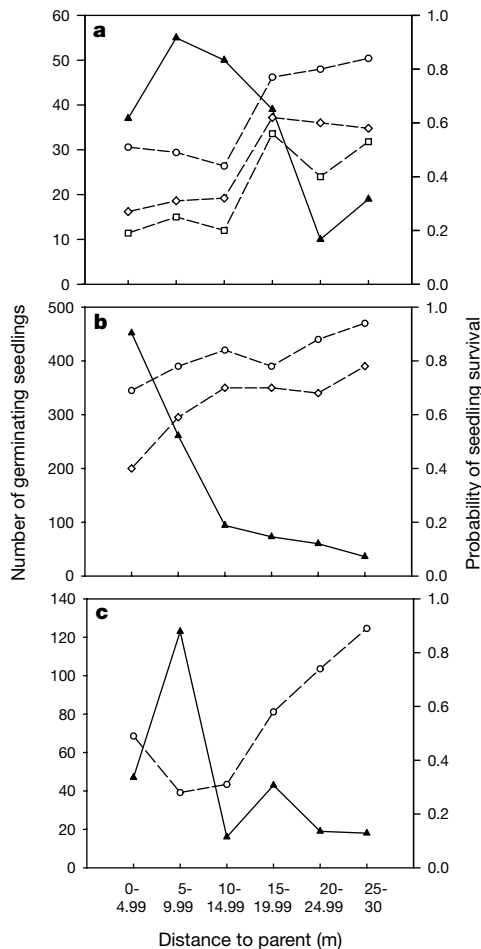


**Figure 1** Relationship between distance to parent, initial seedling germination (filled triangles), and probability of seedling survival over time (dashed lines: open circles, after 4 months; open diamonds, after 16 months; open squares, after 28 months). **a**, Spring 1996 cohorts, $n = 212$ seedlings from beneath 3 trees. **b**, Spring 1997 cohorts, $n = 974$ seedlings from beneath 6 trees. **c**, Spring 1998 cohorts, $n = 266$ seedlings from beneath 3 trees.
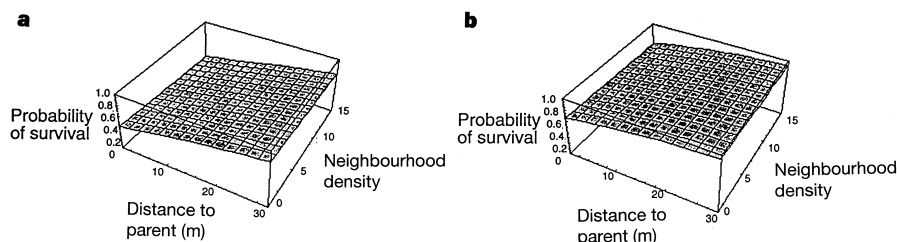


**Figure 2** Logistic regression models of the probability of black cherry survival in relation to distance to parent and neighbourhood density. **a**, Model for seedling survival ($n = 1,455$; Likelihood ratio test: $G = 146$, degrees of freedom (d.f.) $= 2$, $P < 0.00001$). Survival probability is significantly reduced close to the parental tree (Wald statistic $= 57.67$, d.f. $= 1$, $P < 0.00001$, $R = 0.17$, Odds ratio $= 1.06$). Neighbourhood density, although significant in the model, does not strongly influence survival probability (Wald statistic $=$

$45.46$, d.f. $= 1$, $P < 0.00001$, $R = -0.15$, Odds ratio $= 0.97$). **b**, Model for survival of older individuals ($n = 1275$; Likelihood ratio test: $G = 68$, d.f. $= 2$, $P < 0.00001$). Survival probability is significantly reduced close to the tree (Wald statistic $= 45.26$, d.f. $= 1$, $P < 0.00001$; $R = 0.19$; Odds ratio $= 1.07$). Neighbourhood density has no effect on survival (Wald statistic $= 0.32$, d.f. $= 1$, $P = 0.57$).
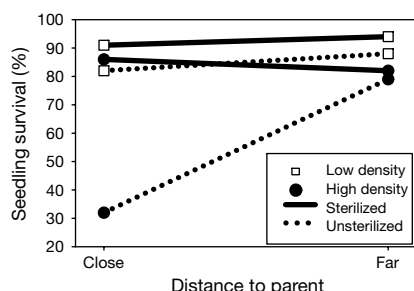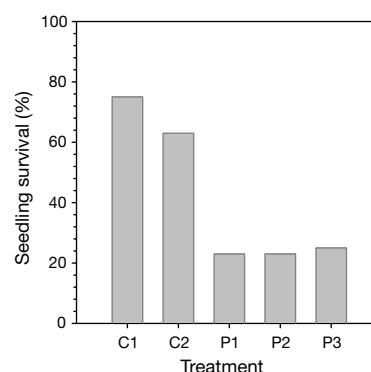
**Figure 3** Effect of distance, neighbourhood density and soil sterilization on black cherry seedling survival. In high density treatments, survival was significantly greater after soil collected close to the tree was sterilized. This effect of sterilization was not found with soil collected further from the tree. The data best fitted a logistic regression model that included density, density × distance, density × sterilization and distance × density × sterilization. Removal of any variable included in the model significantly decreased the model fit (for each variable, $P < 0.0001$).



**Figure 4** Black cherry seedling survival in control and pathogen inoculation treatments ($n = 40$ per treatment). Control 1, potting mix only. Control 2, 5 ml of sterile nutrient-rich fungal growth medium plus potting mix. P1, P2, P3, 5 ml of appropriate inoculum plus potting mix. Survival was significantly lower in pathogen treatments compared with controls after 19 days ($\chi^2 = 13.8$, d.f. = 4, $P < 0.05$).

parent and neighbourhood density at germination were significant predictors of seedling survival, but distance had a stronger effect on survival than density. Survival beneath trees is reduced by 35% relative to survival further away (Fig. 2a). A second model using data from only older individuals also indicated that distance was a better predictor of mortality than density (Fig. 2b). If black cherry root systems support species-specific pathogens, then seedling mortality at a given distance should be relatively constant between years, whereas neighbourhood density may be more variable.

To verify that soil pathogens caused the observed distance- and density-dependent mortality, we conducted a greenhouse experiment using field soil. Independent variables were (1) soil distance (near or far), (2) seedling density (1 or 3 per pot), and (3) soil sterilization (sterilized or not sterilized). There was a three-way interaction between distance, density and sterilization (Fig. 3). In near soil, seedling survival at high density was greatly reduced in unsterilized soil compared with sterilized soil. Seedling survival at high density in far soil was unaffected by sterilization. At low seedling density, survival was unaffected by sterilization, regardless of soil distance. If the pathogen is either at low density or spatially heterogeneous, then the chance of interception by one seedling would be low relative to that of three seedlings, and survival in low density treatments would be high regardless of soil sterilization. Autoclaving soil also kills mycorrhizal fungi and other soil biota, resulting in a nutrient flush. If mycorrhizal fungi enhanced seedling survival beneath the parent tree, sterilized treatments would have reduced seedling survival relative to unsterilized treatments. The opposite effect was observed. Similarly, if a nutrient flush caused the increased survival in sterilized soil, the effect of sterilization would not be distance dependent as we observed. Thus, the results suggest that a soil pathogen causes seedling mortality, especially at near distances and high densities. High seedling density beneath the tree could effectively amplify fungal inoculum such that heavy seed rain would not overwhelm the effects of the pathogen but rather reinforce them, a process opposite to that of predator satiation.

Damping-off type symptoms preceded seedling death in the greenhouse and field. Isolates were obtained from roots of dying seedlings, and the three most common isolates were used to inoculate healthy seedlings. Seedling survival was reduced by an average of 65% in inoculation treatments (Fig. 4). The three isolates were identified as *Pythium* spp. (see Methods) and *Pythium* was later re-isolated from roots of dying seedlings, fulfilling Koch's postulates. Asexual isolates of *Pythium* are difficult to distinguish on the basis of morphological characteristics[26] and will require molecular characterization.

Although *Pythium* spp. are often considered generalist pathogens[27], they appear to differentially affect seedlings of common tree species. In our preliminary study, black cherry seedling mortality was 100% in black cherry soil, whereas mortality of tulip poplar (*Liriodendron tulipifera*) and dogwood (*Cornus florida*) seedlings was low in black cherry soil. The specificity of the pathogen is further supported by field data suggesting that survival of heterospecific seedlings is not impaired under black cherry. Censuses beneath three focal trees (1, 4 and 5) with high densities of black cherry seedlings revealed only 4 black cherry saplings over 0.5 m high within 10 m (basal stem diameter (b.s.d.) = 18.75 ± 0.75 mm). In contrast, 41 saplings of other species were found within 10 m, including multiple individuals of beech (*Fagus grandifolia*, b.s.d. = 36.56 ± 3.04 mm), sugar maple (*Acer saccharum*, b.s.d. = 47 ± 2.29 mm), dogwood (*Cornus florida*, b.s.d. = 28.71 ± 5.20 mm), ash (*Fraxinus* sp., b.s.d. = 19.67 ± 2.96 mm) and eastern hop hornbeam (*Ostrya virginiana*, b.s.d. = 36 ± 3.00 mm). Seedlings of these species were sparse relative to the cherry seedlings, suggesting that their survival is high beneath black cherry adults. Furthermore, only heterospecific adults occurred within the arcs, suggesting that mortality caused by soil pathogens favours heterospecific recruitment despite the high level of black cherry seed dispersal.

The results of our study on a single species demonstrate that the Janzen–Connell mechanism operates within temperate forests. Tropical predators and herbivores are thought to have greater host-specificity than their temperate counterparts[1,28] (but see ref. 29); however, less is known about soil microorganisms in either region. An important goal for future research is to determine how frequently the mechanism proposed in the Janzen–Connell hypothesis operates in temperate compared with tropical communities, and the relative importance of animal predators and herbivores versus microbial pathogens. If a smaller proportion of temperate species is damaged by host-specific natural enemies, then similar distance- and density-dependent processes operating in both temperate and tropical communities may lead to different levels of diversity. □

## Methods

### Demographic censuses

germinating cohorts were followed for arcs established in 1997. Individuals established before the beginning of the study ('older') were included in the census. Thus, there were a total of 6 older cohorts and 12 germinating cohorts (3 from 1996, 6 from 1997 and 3 from 1998).

Censuses were conducted in May and September of 1996, 1997 and 1998. Seedlings' distance to parent and distance to all other seedlings were calculated using $x$, $y$ coordinates. Neighbourhood density was estimated by the number of conspecific seedlings/saplings within a 20 cm radius. Neighbourhood density for individuals along the arc's edge was adjusted by projecting a mirror image of seedling distribution 20 cm within the arc.

## Separating distance and density effects

In logistic regression models, distance to parent and neighbourhood density were entered as independent variables, and seedling status (alive or dead) was entered as the dependent variable. Density at germination was used for seedlings, whereas density at the first census was used for older individuals. Logistic regression analyses were conducted using SPSS, version 6.1.3. Comparisons of mean distance to parent at initial and subsequent census dates were made by generating reliability estimates using Resampling Stats, version 3.14.

## Effect of soil

Fruits were collected from three trees in Bloomington with large crops. Fruit flesh was removed, and seeds were surface sterilized (1 min 70% alcohol, 3 min 50% bleach, 1 min 70% alcohol, 1 min distilled water). To break dormancy, seeds were stratified in wet sterile sand at 4 °C for 5–6 months. Soil was collected at distances of 0–5 m and 25–30 m beneath trees 1, 4 and 6. Soil was sieved and root material was cut into ~1 cm pieces and returned to the soil. Soil samples were diluted 1 : 1 v/v with sterile potting mix (Metro Mix). One half of the soil in each distance class was autoclaved for 4 h at 211 °C. Seedlings that germinated following stratification were planted in each of four soil types (near/far, sterile/unsterile) and watered individually to prevent cross-contamination. Growth and survival of seedlings were monitored for 2 months in the greenhouse. The experiment was conducted in 1998, and again in 1999 with minor modifications. In 1998 all replicates were planted in 4 cm pots, and pots from each soil treatment were placed in the same flat and rotated weekly. In 1999 replicates were planted in randomly distributed 6.5 cm pots. There were no significant differences between years so data from 1998 and 1999 were combined; $n = 34$ per treatment combination except for the treatment combination with both high density and sterilized soil where $n = 28$. Data were analysed using backward conditional logistic regression (SPSS, version 6.1.3).

## Pathogen isolation

Upon seedling death in field soil, roots were surface sterilized for 5 min in a 5% bleach solution and rinsed in distilled water. Cross-sections from the leading edge of the disease lesion were plated on corn-meal agar. Isolates were subcultured and maintained on corn-meal agar plates. Isolates were identified to genus by Karen Rane, Diagnostic Technician at Purdue Plant and Pest Diagnostic Laboratory, West Lafayette, Indiana. *Pythium* spp. are in the division Oomycota, kingdom Protoctista (not true fungi). Isolates are maintained at Indiana University and available on request. The three most common isolates were used to create inocula grown in a nutrient-rich vermiculite medium. Over 80% of all isolates were one of these three (distinguished on the basis of growth rate; colour and texture were similar). Inoculation treatments are referred to as P1, P2, and P3. To obtain seedlings for screening, ~200 seedlings were collected from an abundant population along a woodland/field margin. Seedlings were within 5 m of each other and in a similar microhabitat, and did not occur beneath a black cherry canopy. Roots were rinsed with distilled water to reduce contamination. Although some seedlings may have been infected when collected, seedlings were randomly distributed among treatments. Plastic pots (6.5 cm) were filled with potting soil and watered. Five millilitres of inoculum were added to a depression created in the centre of each pot. Seedlings were planted into this depression and exposed vermiculite was covered. Two controls were included: potting mix only (control 1); and sterile nutrient-rich medium and potting mix (control 2). There were 40 replicates of each treatment and control. Seedlings were removed upon death. The null hypothesis that survival is independent of treatment was tested using the $\chi^2$ test statistic. Roots from plants dying in each treatment were plated on corn-meal agar to determine whether the fungus could be re-isolated from the roots.

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# The ecological cost of sex

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Why sex prevails in nature remains one of the great puzzles of evolution[1,2]. Sexual reproduction has an immediate cost relative to asexual reproduction, as males only express their contribution to population growth through females. With no males to sustain, an asexual mutant can double its relative representation in the population in successive generations. This is the widely accepted 'twofold cost of males'[1–3]. Many studies[4–7] have attempted to explain how sex can recoup this cost from fitness benefits associated with the recombination of parental genotypes, but these require complex biological environments that cycle over evolutionary timescales. In contrast, we have considered the ecological dynamics that govern asexual invasion. Here we show the existence of a threshold growth rate for the sexual population, above