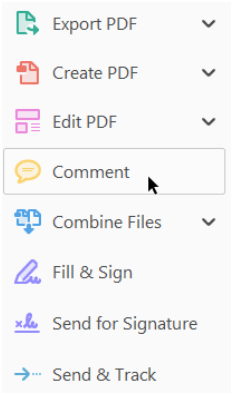
MAKING CORRECTIONS TO YOUR PROOF

These instructions show you how to mark changes or add notes to your proofs using Adobe Acrobat Professional versions 7 and onwards, or Adobe Reader DC. To check what version you are using go to **Help** then **About**. The latest version of Adobe Reader is available for free from get.adobe.com/reader.

DISPLAYING THE TOOLBARS

Adobe Reader DC

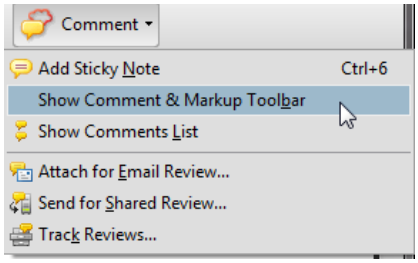
In Adobe Reader DC, the Comment toolbar can be found by clicking 'Comment' in the menu on the right-hand side of the page (shown below).



The toolbar shown below will then display along the top.

Acrobat Professional 7, 8, and 9

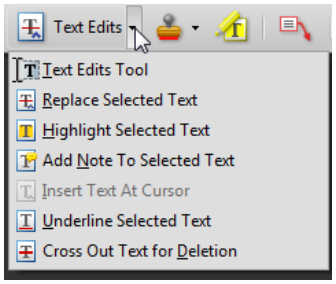
In Adobe Professional, the Comment toolbar can be found by clicking 'Comment(s)' in the top toolbar, and then clicking 'Show Comment & Markup Toolbar' (shown below).



The toolbar shown below will then be displayed along the top.

USING TEXT EDITS AND COMMENTS IN ACROBAT

This is the quickest, simplest and easiest method both to make corrections, and for your corrections to be transferred and checked.



1. Click **Text Edits**
2. Select the text to be annotated or place your cursor at the insertion point and start typing.
3. Click the **Text Edits** drop down arrow and select the required action.

You can also right click on selected text for a range of commenting options, or add sticky notes.

SAVING COMMENTS

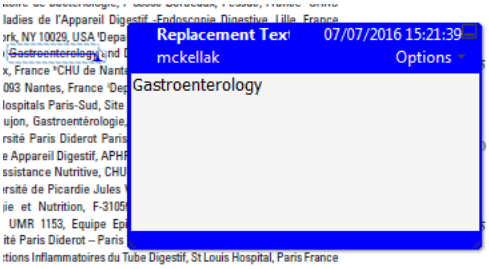
In order to save your comments and notes, you need to save the file (**File, Save**) when you close the document.

USING COMMENTING TOOLS IN ADOBE READER

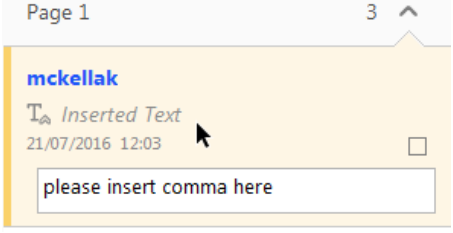
All commenting tools are displayed in the toolbar. You cannot use text edits, however you can still use highlighter, sticky notes, and a variety of insert/replace text options.

POP-UP NOTES

In both Reader and Acrobat, when you insert or edit text a pop-up box will appear. In **Acrobat** it looks like this:



In **Reader** it looks like this, and will appear in the right-hand pane:



DO NOT MAKE ANY EDITS DIRECTLY INTO THE TEXT, USE COMMENTING TOOLS ONLY.

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Frankenstein and the Horrors of Competitive Exclusion

~~XXXXXXXXXX~~

The bicentennial celebration of the inception of *Frankenstein* invites the present view of Victor Frankenstein and his fateful decision to destroy an unfinished female creature. The act itself was impulsive (caused by a "sensation of madness"), but it was preceded by agonized reasoning that would be familiar to any student of ecology or evolutionary biology. Here, we present a formal treatment of Frankenstein's reasoning and show that his rationale for denying a mate to his male creation has empirical justification. ~~It was a prudent decision,~~ because it averted our own extinction by competitive exclusion. ~~Our results suggest~~ that the central horror of Mary Shelley's novel lies in its prescient command of foundational concepts in ecology and evolution.

Some background

Victor Frankenstein created and then disavowed a nameless male creature described as 8 feet in height and proportionally large. For 3 years, the frightened creature wandered the European wilderness, becoming thoughtful, compassionate, and literate in three languages. In a pivotal scene, the creature encounters Frankenstein in Switzerland and pleads for a female companion "of the same species" to mitigate his loneliness. Crucially, and cleverly, the creature anticipates and preempts concerns of direct competition with humans; he promises geographic isolation and emphasizes resource partitioning:

> If you consent, neither you nor any other human being shall ever see us again: I will go to the vast wilds of South America. My food is not that of man; I do not destroy the lamb and the kid to glut my appetite; acorns and berries afford me sufficient nourishment. My companion will be of the same nature as myself, and will be content with the same fare. We shall make our bed of dried leaves; the sun will shine on us as on man, and will ripen our food.

Frankenstein concedes to these assurances and commenced work on a female creature. However, he ~~begins to reflect~~ on the potential for population growth and direct competition: "A race of devils would be propagated upon earth who might make the very existence of the species of man a condition precarious and full of terror." The nature of this terror is clarified when he considers the probability of human extinction: "Future ages might curse me as their pest, whose selfishness had not hesitated to buy its own peace at the price, perhaps, of the existence of the whole human race." Here, we indulge ~~his~~ anguished conjecture by asking whether and when a population of creatures C could drive a population of humans H to extinction.

Modeling species interactions

To model species interactions, we elevated a tacit assumption to a formal parameter by assigning competitive advantages to creatures in a classic Lotka-Volterra competition framework, ~~in which the~~ effect of creatures on humans (which is always harmful by direct or indirect competitive interaction) is a_{HC}, and the effect of humans on creatures is a_{CH}, where $a_{HC} > a_{CH}$ maintains a competitive advantage for creatures. Given growth rates for humans r_H and creatures r_C, as well as a carrying capacity for both k, the two-dimensional continuous time model is written

$$\dot{H} = r_H H(1 - (H + a_{HC}C)/k),$$

$$\dot{C} = r_C C(1 - (C + a_{CH}H)/k),$$

where human extinction is inevitable. However, the time to extinction could be as much as $t_e = 10^8$ years, which is tantamount to species coexistence at biological timescales.

Such an outcome is hardly surprising, given that the global population of humans in 1816 would have exceeded a founding population of two creatures by nine orders of magnitude. The population of Europe was then 178×10^6, whereas the global population was 1.01×10^9 (with an assumed carrying capacity of $k = 10^{10}$). Given a *human growth rate* (= *birth rate – death rate*) of $r_H = 0.0067$, there is little reason for Frankenstein to envision imminent extinction. However, the creature is known to have recovered from a gunshot wound that "shattered flesh and bone," suggesting that reanimated tissue is resistant to necrosis. If undead tissue dies at a slower rate than living human tissue does, then it follows that creatures ~~would~~ have a correspondingly lower death rate, such that the overall growth rate is $r_C = 1.5 \times$ *human growth rate*.

These parameters shed new light on Frankenstein's decision to destroy his unfinished female creature. If we assume direct competition with humans in 1816 and if we allow the competitive advantage of creatures to vary from $\varepsilon = 2\times$ to $\varepsilon = 10\times$ *the competitive effects of humans on creatures*, then we can assess extinction time as a function of competition. In other

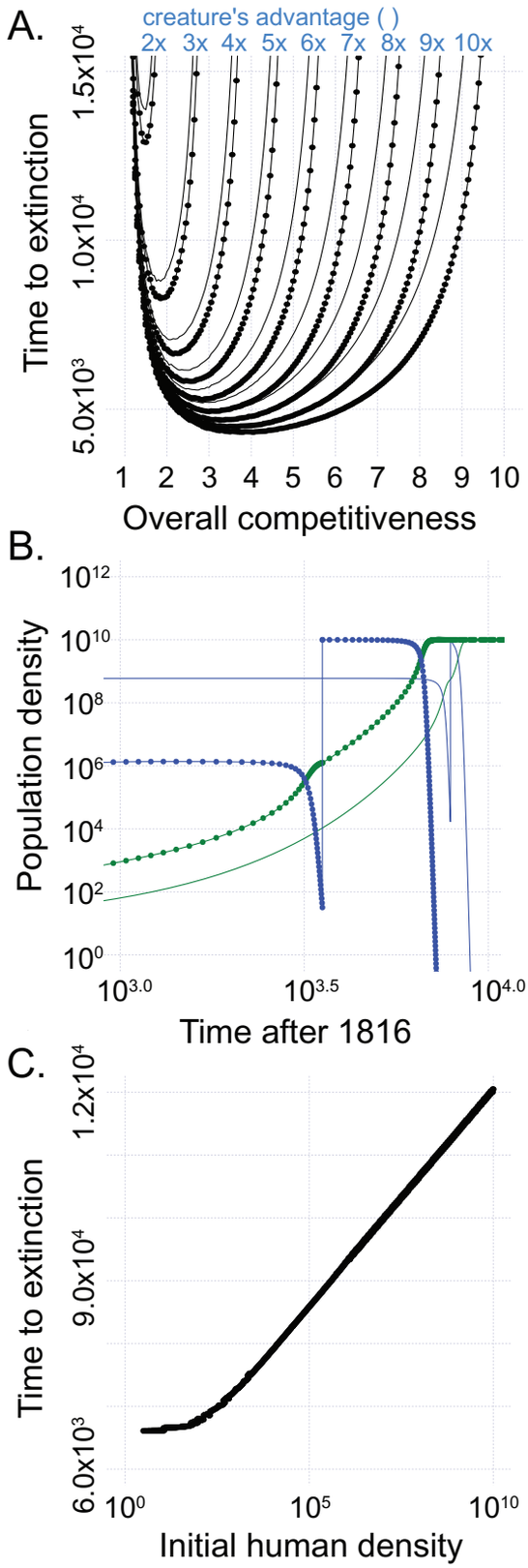

Figure 1. (a) Extinction time given a competitive environment. (b) Population trajectories for humans (descending) and creatures (ascending) given initial growth in the Amazon catchment (~~dotted~~) and Europe (solid). (c) Time to extinction versus the human population size during initial growth of the creature population.

words, $a_{HC} = \varepsilon a_{CH}$, where the effect of creatures on humans is ε× the effect of humans on creatures.

When competition is low, the time to human extinction is effectively infinite, meaning that populations of creatures and humans can coexist (figure 1a). However, as competition increases, our model shows that the time to human extinction drops precipitously to a minimum and then increases, an effect that becomes more exaggerated as the competitive advantages of creatures increase. Intriguingly, if the overall level of competition is high, the creatures are doomed to extinction despite their competitive advantage, such that the time to human extinction is also infinite. This result occurs because the population of creatures begins at $n = 2$ individuals, a population size that is too small for establishing a competitive foothold. In the worst-case scenario for humans ($a_{HC} = 3.5$, $\varepsilon = 10$), our global model indicates human extinction in $t_e = 4188$ years. We invite readers to explore simulations and model results with ~~an interactive online application (using the Mathematica CDF player)~~, available in the supplemental materials.

Dispersal to South America

Given the large demographic disparity between creatures and humans, it is worth considering whether different environmental parameters might alter competitive outcomes. Recall that the creature promised to inhabit "the vast wilds of South America" in an apparent gesture of conciliation. We therefore explored the effects of dispersal to South America by comparing interactions between creatures and humans in the Amazon catchment (~~dotted~~ curves, figures 1a and 1b) and Europe (solid curves, figures 1a and 1b). We assume that when a population of creatures reaches 90 percent of the carrying capacity of either environment, it will begin direct competition with the global human population.

A founding population of two creatures in South America (ascending green ~~dotted~~ line, figure 1b) would quickly surpass the local human population

Mount Tambora and the year without summer.

Recent tributes have renewed interest in the eruption of Mount Tambora in April 1815 and its pernicious aftereffects, particularly the anomalous weather of 1816 (the "year without summer"). The paroxysmal eruption was cataclysmic, ejecting nearly 175 cubic kilometers of volcanic debris, including 50 million tons of sulfur dioxide, which rose into the stratosphere, enveloped the Earth, and oxidized to form small, light-reflecting sulfate particles. The reflection of sunlight reduced the energy absorption of Earth and caused cooler temperatures. In the Northeast United States, summer snow and an unrelenting series of August frosts destroyed crops, caused famine, and gave rise to the colloquialism "eighteen-hundred-and-froze-to-death."

~~The darker skies of 1816~~ contributed to the gloom, conditions that Lord Byron ~~beautifully described~~ as "despairing light" of "mad disquietude." These words appear in one of his most celebrated poems, fittingly titled "Darkness." The ~~dire~~ mood of 1816 is familiar to students of Victorian literature for its influence on many writers, including Byron and Percy Bysshe Shelley, who were then visiting Lake Geneva, Switzerland, with a literary coterie that included Mary Shelley, Mary's stepsister Claire Clairmont, and the physician John Polidori. The inclement conditions drove the party indoors; it was, in Mary's words, "a wet, ungenial summer [of] incessant rain." Fireside gatherings in the Villa Diodati (pictured) led to the reading aloud of ghost stories and Byron's challenge to each person to write their own ghostly tale. For Mary, the proposition provoked a "waking dream" (probably 16 June 1816) that eventually gave rise to *Frankenstein*, published in 1818, whereas John Polidori produced *The Vampyre*, published in 1819. The characters and gothic tone of these works have had a large influence on popular culture, a volcanic byproduct that continues two centuries on.

(~~descending~~ blue ~~dotted~~ line, figure 1b; the vertical jump denotes the transition from regional to global competition) and drive humans to extinction faster than competition in Europe (creatures: ascending green solid line; humans: ~~descending~~ blue solid line; figure 1b). The lower t_e for this scenario holds across all levels of competition and for all values of ε (~~dotted~~ curves, figure 1a). The wilds of South America would therefore accelerate the population growth of creatures, at least compared with the slower dynamics that would have occurred in Europe, with its larger human population. In general, we find that low-density—and, by extension, low-competition—initial environments can catalyze the establishment of an invading population, thereby hastening the extinction of a resident population (figure 1c).

The present findings are drawn from a work of science fiction, but

their importance is threefold. First, our results reinforce and expand the gothic tone of *Frankenstein* and its underlying exploration of moral and scientific responsibility. Second, our results cast new light on the creature and his motives for inhabiting the wilds of South America, a lower-competition environment. Third, our results bolster the speculative concerns of Frankenstein with empirical support: Humans would indeed face species interactions "full of terror." The nature of this terror is termed *competitive exclusion*, a concept that escaped definition until the 1930s. We conclude by suggesting that the central horror and genius of Mary Shelley's novel lie in its early mastery of foundational concepts in ecology and evolution.

Acknowledgments

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