BIODIVERSITY RESEARCH

Native communities determine the identity of exotic invaders even at scales at which communities are unsaturated

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ABSTRACT

Aim To determine why some communities are more invasible than others and how this depends on spatial scale. Our previous work in serpentine ecosystems showed that native and exotic diversity are negatively correlated at small scales, but became positively correlated at larger scales. We hypothesized that this pattern was the result of classic niche partitioning at small scales where the environment is homogeneous, and a shift to the dominance of coexistence mechanisms that depend on spatial heterogeneity in the environment at large scales.

Location Serpentine ecosystem, Northern California.

Methods We test the above hypotheses using the phylogenetic relatedness of natives and exotics. We hypothesized that (1) at small scales, native and exotic species should be more distantly related than expected from a random assemblage model because with biotic resistance, successful invaders should have niches that are different from those of the natives present and (2) at large scales, native and exotic species should not be more distantly related than expected.

Result We find strong support for the first hypothesis providing further evidence of biotic resistance at small scales. However, at large scales, native and exotic species were also more distantly related than expected. Importantly, however, natives and exotics were more distantly related at small scales than they were at large scales, suggesting that in the transition from small to large scales, biotic resistance is relaxed but still present. Communities at large scales were not saturated in the sense that more species could enter the community, increasing species richness. However, species did not invade indiscriminately. Exotic species closely related to species already established the community were excluded.

Main conclusions Native communities determine the identity of exotic invaders even at large spatial scales where communities are unsaturated. These results hold promise for predicting which species will invade a community given the species present.

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INTRODUCTION

Biological invasions are one of the largest ecological and economic problems we face. Invasive species represent one of the most significant threats to biological diversity, along with habitat loss and fragmentation (Wilcove *et al.*, 1998; Pimentel *et al.*, 2000). Thus, any knowledge we can contribute to understanding the process of invasion will have huge benefits

for humanity. In particular, identifying the factors that make communities more or less invasible is critical.

Why some communities are more invasible than others and how this can depend on the spatial scale at which we observe them are questions that have long intrigued ecologists (Levine *et al.*, 2004; Davies *et al.*, 2005; Fridley *et al.*, 2007; Diez *et al.*, 2008; Stohlgren *et al.*, 2008; Cadotte *et al.*, 2009). These questions underlie fundamental concepts in community

ecology: species coexistence and assembly (Chesson, 2000a,b; Tilman, 2004). Therefore, their exploration continues to offer insights into why communities are structured the way they are. Further, questions about the invasibility of communities are of both great conservation and economic importance.

When communities are observed and manipulated at small spatial scales, we tend to detect negative relationships between native and exotic diversity (Elton, 1958; Turelli, 1981; Case, 1990; Tilman, 1997; Knops *et al.*, 1999; Stachowicz *et al.*, 1999; Levine, 2000; Naeem *et al.*, 2000; Lyons & Schwartz, 2001; Brown & Peet, 2003; Davies *et al.*, 2005), suggesting that native diversity armours a community against invasion. In contrast, when communities are observed at large spatial scales, we tend to detect positive relationships between native and exotic diversity, suggesting that diverse communities are more invasible (Lonsdale, 1999; Stohlgren *et al.*, 1999, 2008; Davies *et al.*, 2005, 2007a,b; Richardson *et al.*, 2005). This has been referred to as the diversity–invasibility paradox. Previously, Davies *et al.* (2005) suggested that negative relationships tend to be detected at scales at which the environment and resources are relatively homogenous and classic niche partitioning (and competitive exclusion) dominate (Grime, 1973; Tilman, 1999). We suggested that the relationship between native and exotic diversity becomes positive at scales at which spatial heterogeneity in the environment is such that coexistence mechanisms that depend on heterogeneity become dominant, resulting in communities that could be considered 'unsaturated'. A comprehensive review of the paradox (Fridley *et al.*, 2007) came up with a similar framework built on the shift from biotic to abiotic drivers as scale increases. Eight processes that could generate either negative or positive relationships were identified, but all could be fitted within their framework.

The new field of community phylogenetics has allowed ecologists to use information about evolutionary relatedness of species within communities to understand invasibility (Strauss *et al.*, 2006; Proches *et al.*, 2008; Cadotte *et al.*, 2009). Ideas from this field have strong analogues with ideas about diversity, invasibility and scale (Davies *et al.*, 2005; Fridley *et al.*, 2007; Melbourne *et al.*, 2007). At small spatial scales, native species are likely to resist invasion of closely related invaders because they are likely to occupy similar niches. Density dependent factors associated with limiting similarly are hypothesized mechanisms, including effects of competition, and predator, pathogen and disease resistance (Webb *et al.*, 2002, 2006; Cavender-Bares *et al.*, 2004, 2009; Strauss *et al.*, 2006; Davies *et al.*, 2007a,b; Gilbert & Webb, 2007). Thus, coexisting species should be phylogenetically more distantly related than a random assemblage model. In contrast, at large scales, coexisting species should be more closely related than expected because of the effect of environmental filtering on membership of regional communities (Cavender-Bares *et al.*, 2006; Swenson *et al.*, 2006, 2007; Willis *et al.*, 2009). Considering relationships between native and exotic species, Darwin's naturalization hypothesis is an analogue of the small scale hypothesis but considers genera rather than species. It suggests that exotic genera with no close relatives in a new area are more likely to colonize than exotic genera with close relatives, because of the lack of competitive exclusion (Darwin, 1859). An important issue is the extent to which phylogenetic relatedness provides information about ecological similarity and niche overlap. While there is evidence for trait similarity and niche conservatism in plants (Ackerly & Reich, 1999; Prinzing *et al.*, 2001; Kerkhoff *et al.*, 2006; McCarthy *et al.*, 2007), it is often the case that within groups of close relatives (e.g. oak species or anolis lizards), species are labile in functionally important ways, and phylogenetic relatedness does not predict ecological similarity (e.g. Cavender-Bares *et al.*, 2004; Losos, 2008). At increasing phylogenetic scales, such as those encompassed in diverse plant communities that include many distinct lineages, phylogenetic relatedness of species is likely to be more predictive of ecological similarity (Cavender-Bares *et al.*, 2006, 2009; Swenson *et al.*, 2006, 2007). Disease resistance, for example, is well predicted in experimental studies by phylogenetic distance between hosts (Gilbert & Webb, 2007). In general, if traits evolve according to a Brownian motion model of evolution, greater divergence in trait values between species is expected with a longer time since divergence (e.g. Butler & King, 2004; Losos, 2008; Ackerly, 2009). To the extent that phylogenetic relationships provide reasonable information about the evolutionary relationships among species and their divergence times, the phylogenetic distances between species provide an integrated estimate of the relative magnitude of the genetic and phenotypic differences between species.

Phylogenetic distances between species may thus provide an estimate of the ecological similarity and niche overlap of species and therefore help us to predict which species are more or less likely to invade a community given which species are present and their phylogenetic relationships to potential invaders. Several invasion studies have found the phylogenetic relatedness of native species to exotics to be an important predictor of invasion success. In California, successful exotic grass invaders were significantly less phylogenetically related to native species in new geographic areas compared with non-invasive exotic species (Strauss *et al.*, 2006). In New Zealand, the proportion of introduced species that become naturalized is higher for plants that have native congeners than for those that do not (Duncan & Williams, 2002). A species-addition experiment in prairie grasslands showed that established species most strongly inhibited introduced species from their own functional group so that there was greater competitive inhibition of invaders that were similar to established abundant species (Fargione *et al.*, 2003). None of these studies considers the effects of scale. However, Cadotte *et al.* (2009) examined the occupancy of exotic plant species in Royal National Park, Australia and then also examined the occupancy of those exotic species at a continental scale using herbarium records. Natives and exotics were more closely related than expected at large scales, suggesting that invaders and natives share ecological traits that make them successful. At small scales, exotics were neither more nor less closely related.

In Californian serpentine plant ecosystems, we found negative relationships between native and exotic diversity at small scales, and positive relationships at large scales (Davies *et al.*, 2005). We defined diversity as species richness. We demonstrated that the observed relationship between native and exotic diversity flipped from negative to positive at scales at which spatial heterogeneity in the environment came into play (was correlated with native and exotic diversity and beta diversity). We hypothesized that this is because at small scales, the environment is homogeneous and biotic interactions dominate, whereas at large scales, spatial heterogeneity in the environment increases and coexistence mechanisms that depend on spatial heterogeneity in the environment dominate. Recent experiments showed that phylogenetic clustering increases with spatial scale but also with experimental increases in the heterogeneity in the environment within the same spatial scale (Willis *et al.*, 2009). We expect that the predicted effects are not dependent on spatial scale *per se*, but rather on the fact that heterogeneity in the environment almost always increases with increasing scale (Davies *et al.*, 2005). Here, we test these hypotheses using the phylogenetic relatedness of natives and exotics in the same system. Given our findings for diversity, we hypothesized that (1) at small scales, native and exotic species should be more distantly related than expected from a random assemblage model if there is biotic resistance as successful invaders should have niches that are different from those of the natives present. The idea of biotic resistance is that direct and indirect interactions between resident species and an invader can make it difficult for an invader to invade. (2) At large scales, native and exotic species should not be more distantly related than expected, or may even be more closely related than expected if the environment filters membership of communities.

METHODS

Data collection

Our survey site was located in patchy serpentine and non-serpentine grassland in the McLaughlin University of California Reserve (38°51′N, 123°30′W), 120 km north of San Francisco, California. We collected data at 96 sites that comprised a 550 × 350-m grid, in the spring of 2001 and 2002. Sites were located 50 m apart in 12 rows and eight columns. At each site, we collected plant composition data in four 1-m square quadrats, located around a central marker. We detected 156 grass and forb species, of which 112 species were native and 44 species were exotic.

For this work, we considered two spatial scales: (1) nine sites within each block (site: 16 m²) and (2) 12 blocks within the grid (block: 10,816 m²). Ideally, the local scale is the scale at which individuals interact with individuals of their own and other species. Operationally, we defined this as the smallest spatial unit, although the scale of interactions may have been smaller than this. In a previous paper from which this work originated (Davies *et al.*, 2005), we considered an additional two spatial scales. For simplicity, we consider only two scales

here, but these encompass the relationships presented in Davies *et al.* (2005).

Creating the phylogenies

A literature-based phylogeny was constructed using the Davies *et al.* (2004) angiosperm supertree from the total species using Phylomatic (Webb *et al.*, 2004) (Fig. 1). Taxon names were initially checked for synonyms to match standardized names from the integrated taxonomic information system (ITIS) using Nix (Kembel, 2007). In groups where intra-generic resolution from the backbone phylogeny was low, polytomies were resolved with branching arrangements from recently published literature. Branching patterns were manipulated in Mesquite version 2.6 (Maddison & Maddison, 2006) based on the phylogenetic hypotheses presented by Panero & Funk (2008) for Asteraceae, Downie *et al.* (2000) for Apioideae, McMahon & Sanderson (2006) for Papilionoid Legumes and Bouchenak-Khelladi *et al.* (2008) for Poaceae. Inclusion of these published relationships within clades increased resolution of the tips of the phylogeny to 56% from 62% based on the Davies *et al.* (2004) tree alone. Branch lengths were estimated using the branch length adjustment algorithm (BLADJ) in Phylocom version 4.0.1 (Webb *et al.*, 2008) using minimum ages from the fossil record from Wikstrom *et al.* (2001). While there are known limitations to the reliability of branch lengths estimated using this approach (Webb *et al.*, 2008), it represents an important advance over methods that use nodal distances as proxies for branch lengths. This literature-based phylogeny takes advantage of existing phylogenetic data, synthesizing published expert knowledge, without the considerable expense and time involved in developing molecular phylogenies.

Data analysis

We used R (R Development Core Team, 2007) for all analyses. We used the sum of phylogenetic diversity (Faith, 1992; Webb, 2000; Webb *et al.*, 2002; Cadotte *et al.*, 2008, 2009) calculated as:

$$d_k^* = \sum_i \sum_j d_{ij}$$

where d_{ij} is the phylogenetic distance between native species i and exotic species j. Our metric was d^* the mean summed distance across sites or blocks, where n is the number of sites or blocks:

$$d^* = \frac{1}{n} \sum_k d_k^*.$$

Phylogenetic distance between natives and exotics

Native versus exotic phylogenetic distance at two spatial scales (sites and blocks)

We asked: is the phylogenetic distance between natives and exotics greater than expected (for both small and large scales)?

Figure 1 Phylogeny of serpentine plant ecosystem community ($n = 152$). Filled circles at the tips of the phylogeny indicate native species, open circles indicate exotics species. Radially extending branch lengths are drawn proportional to distance.

We calculated the observed phylogenetic distance between natives and exotics by calculating the phylogenetic distance between every pair wise combination of natives and exotics in the site or block of interest and then calculating the sum. Across the entire grid, we then took the mean of this number to give one value that represented overall site or block phylogenetic distance between natives and exotics (observed phylogenetic distance). We then compared this observed phylogenetic distance between natives and exotics to those from 10,000 randomizations where we randomly shuffled the species occurrence matrix. We established that our null model had no inherent bias as outlined in Appendix S1.
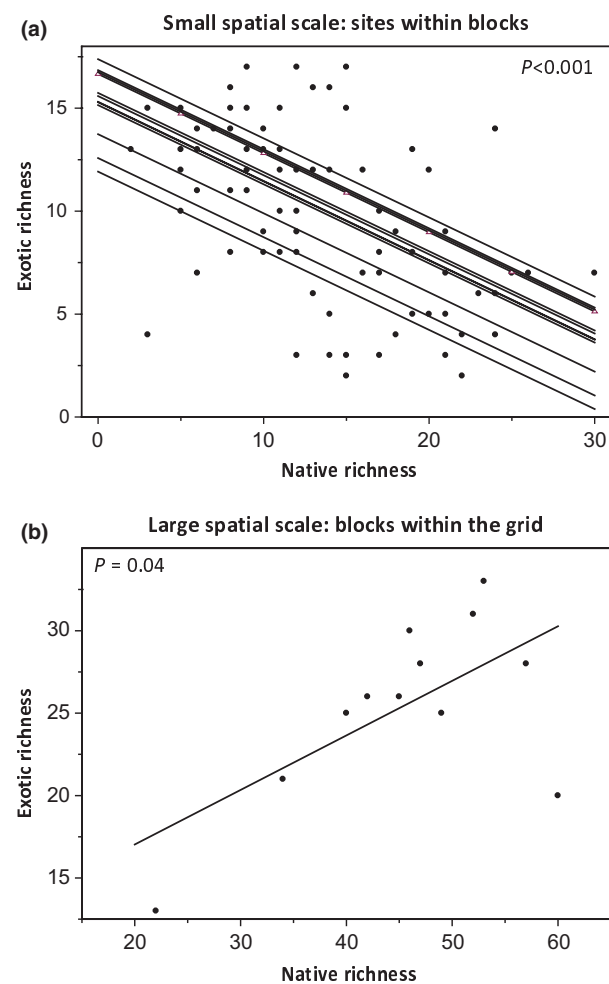
RESULTS

A phylogenetic distance between natives and exotics

In communities at small scales, native and exotic species were significantly more distantly related than expected supporting hypothesis one (observed distance 31,693.06; 95% CI of the expected distances under the null model 27,411.28, 29,964.48). In contrast, we found no support for hypothesis two that at large scales, phylogenetic distance between natives and exotics should be equal to or greater than expected. Instead, at large scales, we found that native and exotic species were more

distantly related than expected (observed distance 30,6340.10; 95% CI of the expected distances under the null model 24,8407.25, 27,4654.47). We also tested whether the distance between natives and exotics was significantly greater at small than large spatial scales and determined that it was greater ($P < 0.001$).

DISCUSSION

As predicted, at small scales, native and exotic species were more distantly related than expected, while in contrast to our predictions, at large scales, native and exotic species were also more distantly related than expected. The small scale result provides support for the hypothesis that native and exotic diversity are negatively correlated at small scales where biotic resistance is the dominant mechanism influencing community assembly (Davies *et al.*, 2005) (Fig. 2a). At large scales, we previously found that native and exotic diversity were positively correlated (Davies *et al.*, 2005) (Fig. 2b). We hypothesized that the relationship flips from negative to positive at scales where spatial heterogeneity in the environment is large and where coexistence mechanisms that depend on spatial heterogeneity in the environment dominate. In our earlier study, this hypothesis was supported by a positive relationship of spatial environmental variance with native and exotic diversity and beta diversity. These earlier findings are consistent with theoretical perspectives about the invasibility of communities and scale (Fridley *et al.*, 2007; Melbourne *et al.*, 2007). Our contrasting results here using phylogenetic diversity suggest that there is more to the story at large scales. We elaborate on this in the following two paragraphs.

Native and exotic species were more distantly related than expected at both small and large scales. However, natives and exotics were more closely related at large than small scales, suggesting that community resistance to invasion was lower at large scales. Thus, as we move from small scales to large scales, biotic resistance is relaxed but is still operating at large scales. The richness results and phylogenetic distance results tell us about different things: richness about how many native and exotic species can coexist with each other and phylogenetic distance about how the extent of shared evolutionary history influences which species can coexist with each other. At large scales, heterogeneity allows species to coexist to the extent that locations that are good for natives also have more exotic species, and communities appear unsaturated. However, resistance to invasion is maintained so that certain species are excluded: those exotic species that are phylogenetically closely related to the species already established in the community.

Recently, Stohlgren *et al.* (2008) suggested that invasion, rather than diminishing the diversity of native species in a community, has the overall effect of increasing the diversity of communities by adding exotic species. They based their conclusion on evidence that communities are unsaturated at large spatial scales and, at least for plants, a lack of species extinctions driven by competitive interactions. Consequently, we should generally find positive relationships between native and exotic diversity at large scales. Stohlgren *et al.* (2008) suggest that ultimately competition appears to play no role in structuring communities at large scales, even if competition is important in structuring communities at small scales and thus is of little interest to invasion studies. However, our results directly contradict this finding by illustrating that even when native and exotic diversity are positively correlated, suggesting lack of saturation, biotic resistance to invasion still structures communities. Exotic species that are phylogenetically closely related to the species already established in the community are excluded (see also Harrison, 2008).

A recent study, similar to our study, examined the relationship between phylogenetic distance between native and exotics at multiple spatial scales and found no phylogenetic signal at small scales, but detected phylogenetic clustering at large scales, suggesting that invaders and natives share ecological traits that make them successful at large scales (Cadotte *et al.*, 2009). This pattern provides evidence for environmental filtering, as has been shown in other studies (Cavender-Bares *et al.*, 2006; Swenson *et al.*, 2006; Willis *et al.*,

(a)

Small spatial scale: sites within blocks

$P<0.001$

Exotic richness (y-axis: 0, 5, 10, 15)
Native richness (x-axis: 0, 10, 20, 30)

(b)

Large spatial scale: blocks within the grid

$P = 0.04$

Exotic richness (y-axis: 15, 20, 25, 30)
Native richness (x-axis: 20, 30, 40, 50, 60)

Figure 2 Relationships between native diversity and exotic diversity at two spatial scales: (a) sites within blocks and (b) blocks within the entire grid.

[3] 2009). The scales considered by Cadotte *et al.* (2009) were larger than those considered here (continent and regional scale versus regional and local scale in our study), and this likely explains the differences in our findings.

The observed phylogenetic distances between native and exotic species not only offer insights into the invasibility of communities but also offer insights into why communities are structured the way they are. Our results confirm that communities are structured not only by biotic resistance but also by environmental heterogeneity (Chesson, 2000a,b), and further, that while competition and heterogeneity interact, they also operate at different scales (local versus regional), at least in [4] plant communities (Chesson, 2000a,b; Chesson *et al.*, 2005). Finally, we find that communities can appear unsaturated but still be structured by biotic resistance.

In summary, ultimately, the phylogenetic identity of species predicted which species were able to invade communities, even at large spatial scales, offering an important illustration of the predictive power of phylogeny in ecological studies (Cavender-Bares *et al.*, 2009). With knowledge of which species are present in the community and phylogenetic relationships to potential invaders, there is potential to predict which species are more or less likely to invade a community in other systems. Intriguingly, we found that as we move from small scales to large scales, the effect of biotic resistance is relaxed but is still present at large scales. Environmental heterogeneity allows species to coexist to the extent that locations that have many niches for native species also have many niches for exotic species, but biotic resistance is still acting so that exotic species that are closely related to native species already established in the community are excluded. In other words, at large scales, even when native and exotic diversity are positively correlated, suggesting lack of saturation, biotic resistance to invasion still structures communities. Future research should determine at which spatial scales the effects of biotic resistance dissipate so that exotics closely related to the species in a given community are no longer excluded. What occurs at these scales that causes these effects to disappear? Further, how broadly do our results apply to other systems?

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SUPPORTING INFORMATION

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

Appendix S1 Test for null model bias.

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# USING E-ANNOTATION TOOLS FOR ELECTRONIC PROOF CORRECTION

Required Software

Adobe Acrobat Professional or Acrobat Reader (version 7.0 or above) is required to e-annotate PDFs. Acrobat 8 Reader is a free download: http://www.adobe.com/products/acrobat/readstep2.html

Once you have Acrobat Reader 8 on your PC and open the proof, you will see the Commenting Toolbar (if it does not appear automatically go to Tools>Commenting>Commenting Toolbar). The Commenting Toolbar looks like this:
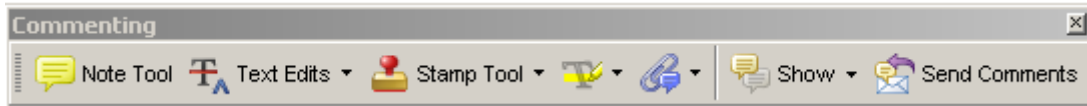
If you experience problems annotating files in Adobe Acrobat Reader 9 then you may need to change a preference setting in order to edit.

In the "Documents" category under "Edit – Preferences", please select the category 'Documents' and change the setting "PDF/A mode:" to "Never".
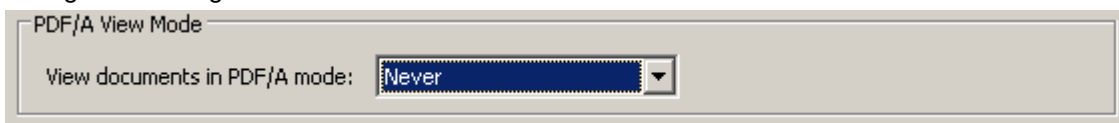
Note Tool — For making notes at specific points in the text

Marks a point on the paper where a note or question needs to be addressed.
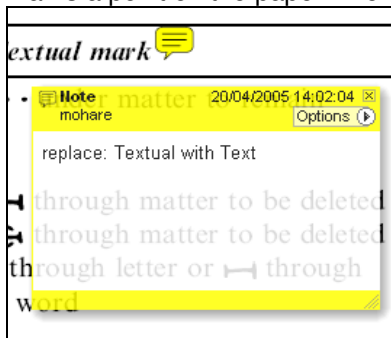
How to use it:
1. Right click into area of either inserted text or relevance to note
2. Select Add Note and a yellow speech bubble symbol and text box will appear
3. Type comment into the text box
4. Click the X in the top right hand corner of the note box to close.

Replacement text tool — For deleting one word/section of text and replacing it

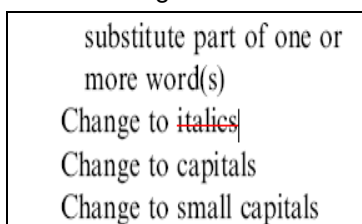Strikes red line through text and opens up a replacement text box.
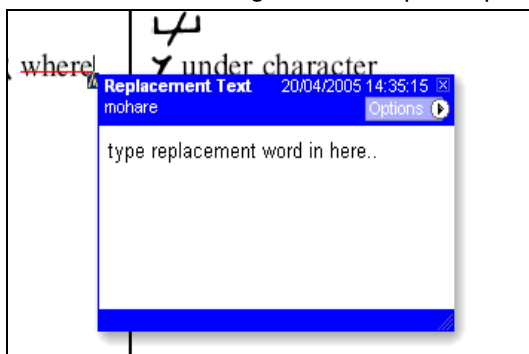
How to use it:
1. Select cursor from toolbar
2. Highlight word or sentence
3. Right click
4. Select Replace Text (Comment) option
5. Type replacement text in blue box
6. Click outside of the blue box to close

Cross out text tool — For deleting text when there is nothing to replace selection

Strikes through text in a red line.

How to use it:
1. Select cursor from toolbar
2. Highlight word or sentence
3. Right click
4. Select Cross Out Text

## Approved tool — For approving a proof and that no corrections at all are required.

How to use it:

1. Click on the Stamp Tool in the toolbar
2. Select the Approved rubber stamp from the 'standard business' selection
3. Click on the text where you want to rubber stamp to appear (usually first page)

Highlight tool — For highlighting selection that should be changed to bold or italic.

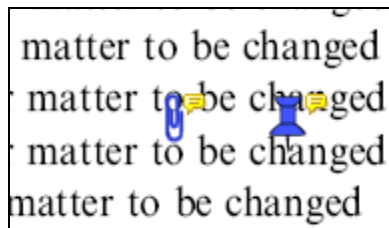Highlights text in yellow and opens up a text box.
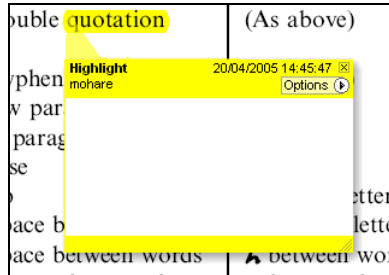
How to use it:

1. Select Highlighter Tool from the commenting toolbar
2. Highlight the desired text
3. Add a note detailing the required change

Attach File Tool — For inserting large amounts of text or replacement figures as a files.

Inserts symbol and speech bubble where a file has been inserted.

How to use it:

1. Click on paperclip icon in the commenting toolbar
2. Click where you want to insert the attachment
3. Select the saved file from your PC/network
4. Select appearance of icon (paperclip, graph, attachment or tag) and close

Pencil tool — For circling parts of figures or making freeform marks

Creates freeform shapes with a pencil tool. Particularly with graphics within the proof it may be useful to use the Drawing Markups toolbar. These tools allow you to draw circles, lines and comment on these marks.
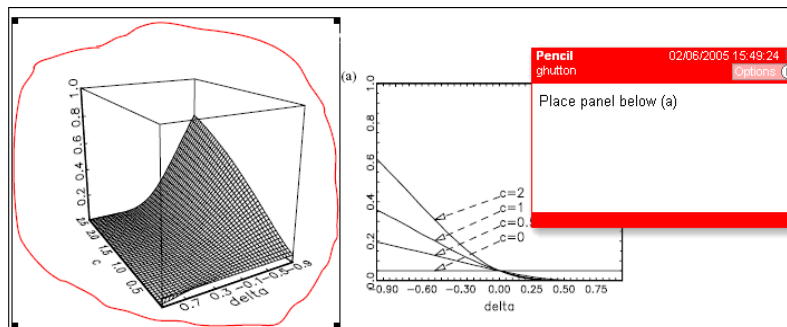
How to use it:

1. Select Tools > Drawing Markups > Pencil Tool
2. Draw with the cursor
3. Multiple pieces of pencil annotation can be grouped together
4. Once finished, move the cursor over the shape until an arrowhead appears and right click
5. Select Open Pop-Up Note and type in a details of required change
6. Click the X in the top right hand corner of the note box to close.

Help

For further information on how to annotate proofs click on the Help button to activate a list of instructions: