Plant functional group responses in an African tropical forest recovering from disturbance

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Introduction

Current rates of tropical forest loss of around 8% per decade (MEA 2005; FAO 2014) are leading to increased efforts to protect and restore previously degraded or disturbed forest (Lamb et al. 2005; Chazdon et al. 2009; Melo et al. 2013). Encouragingly, some tropical forests have been restored successfully by the protection of previously disturbed or deforested land and subsequent recovery of forest structure and function through natural processes.

The impact of disturbance and the progress of restoration or recovery is often assessed based on a selection of taxonomic groups assumed to be useful indicators of overall forest biodiversity (Lawton et al. 1998), as exhaustive biological surveys are resource-intensive (de Andrade et al. 2014). The question is whether the chosen group can represent other taxa present. Arthropods are commonly used indicator taxa in tropical forests (Lawton et al. 1998; Lewandowski et al. 2010), but trees (e.g. Tuomisto et al. 1995; de Andrade et al. 2014), ferns (e.g. Oldekop et al. 2012) and particular families of flowering plants (e.g. Moritz et al. 2001; Ruokolainen et al. 2007) have also been used. In general, the utility of different plant groups as indicators for one another may be challenging due to their different environmental responses and physiological constraints (Pharo et al. 1999; Saure et al. 2014). Still, strong congruence between plant taxa has been found in Amazonia at several spatial scales for ferns, Melastomataceae, trees and shrubs (Tuomisto et al. 1995; Vormisto et al. 2000; Ruokolainen et al. 2007). In Africa, studies have indicated good (Hall and Swaine 1976), intermediate (Pomeroy 1993; Mysal and Horsak 2014) and poor (Decocq et al. 2014) effectiveness of trees as indicators for other forest taxa, but Africa is nevertheless underrepresented in the tropical forest disturbance/restoration literature (Deikumah et al. 2014).

Indicator taxa are most effective at representing other taxa when the abiotic environment is a key determinant of community structure (Ruokolainen et al. 2007; Sætersdal and Gjerde 2011). Disturbance of forests, as a form of abiotic influence, could thus be expected to strengthen the relationship between community structure of different groups, aligning the responses of various taxonomic groups with one another, but several studies on disturbance have found this not to be the case (e.g. Lawton et al. 1998; Saure et al. 2013). There are several reasons why plant species groups might not respond to disturbance in a similar manner. Life history, dispersal ability and interspecific interactions have all been shown to affect recovery from disturbance; where such traits are consistent within groups but contrasted across groups, indicator taxa are expected to perform poorly (Pharo et al. 1999; Saure et al. 2014). Timber harvesting removes individual trees and damages or kills nearby smaller plants (Duncan and Chapman 2003; Mwavu...
and Witkowski 2008). Species with short generation times and good dispersal capacity should recover from disturbance faster, that is, one would expect herb populations to recover faster than late-successional trees. Depending on the type of disturbance, a subset of species may regenerate rapidly from a propagule bank in the soil. This applies primarily to pioneer tree species (Chapman and Chapman 1997; Butler and Chazdon 1998; Dainou et al. 2011), but tropical forest soils also contain herb and shrub seeds and fern spores (Ranalan 2003; Esaete et al. 2014). Recovery rate is also mediated by the environmental tolerances of the species. Forest clearance increases soil exposure (Jonsson and Esseen 1998), soil nutrient availability and light availability (Denslow et al. 1998; Decoq et al. 2004) but reduces moisture (Didham and Lawton 1999; Pohlmian et al. 2007). Ferns are particularly sensitive to microclimate and microtopography with a clear requirement for moisture (Karst et al. 2005; Jones et al. 2006; Flinn 2007) and so forest ferns are often slower to recover from disturbance than herbs (Mabry and Fraterrigo 2009; Larrea and Werner 2010). However, angiosperms may have co-evolved interactions with pollen or seed vectors (Barrington 1993) which may take time to re-establish.

In this paper, we addressed how species richness and compositional patterns change with time since large-scale forest logging and clearance ceased, in different plant groups: large trees, understorey saplings and shrubs (collectively referred to as subcanopy woody species), herbs and ferns. Our study system was the Mabira Forest in Uganda, a 300 km² National Forest Reserve established in 1990 on the basis of its tree, bird and butterfly diversity (Howard et al. 2000). Mabira Forest consists of a mosaic of patches ranging from areas not affected by logging since before the 1950s and never clear-felled to areas used for agriculture throughout the 1980s and which have been left to regenerate only relatively recently. According to previous studies in Uganda, forest plant species groups show different rates of recovery from disturbance: Mucunguzi (2007) found no difference in the species diversity of epiphyte communities between disturbed and undisturbed forest 25 years after logging, while Plumptre (1996) found that tree communities were still affected by selective arbocide use 60 years after application.

We predicted that because different ecological drivers (e.g. disturbance, microclimate) are the most important for each of the different plant functional groups, the patterns of similarity and dissimilarity between sites are not likely to be consistent for the different groups. Instead, the importance of forest history versus local environment would vary in predictable ways, with the longer-lived large trees showing a stronger response to disturbance, and the well-dispersed ferns showing the strongest response to local environment (e.g. light, leaf litter depth). Furthermore, as a conservation objective, we explored recovery of the forest from past disturbance and asked whether species restricted to forests (as opposed to generalists and weeds) are reappearing and/or increasing in the regenerating forest.

Materials and methods

Study area

Mabira Central Forest Reserve (hereon Mabira) is in central Uganda at 0° 24’ N 33° 01’ E, close to Lake Victoria (Figure 1). The climate is tropical with two rainfall peaks (April to May and October to November). Mean annual temperature is 28°C (Ministry of Water Lands and Environment 2002) and annual rainfall is 1250–1400 mm (Howard 1991). The forest covers about 300 km² over an elevational range of 1070–1340 m above sea level. The topography is gently undulating with numerous flat-topped hills and shallow valleys. The soils are sandy loam with clays in the valleys (Howard 1991). The forest is isolated from other protected areas and large forests by agricultural land.

Mabira is a semi-deciduous secondary forest, highly influenced by human activities. About 95% of the forest is of the Celtis-Chrysophyllum medium altitude semi-deciduous forest communities and 5% is Piptadeniastrum-Albizia-Celtis communities. We focused on the former: within this there are stands of different ages which have developed since the forest underwent phases of felling and encroachment (Howard 1991; Davenport et al. 1996).

Commercial exploitation of Mabira began in 1906 (Howard 1991). Between 1906 and 1950, the western block (36% of the total area) was subjected to selective logging on an extensive scale, where individual trees were removed and surrounding trees suffered high levels of damage (Hamilton 1984); this area is now in an advanced stage of regeneration. Another portion on the eastern side was lightly pit-sawn with between 6% and 70% of the valuable timber (mature Milicia spp. and Entandrophragma spp.) selectively logged during this period (Howard 1991). After 1950, a large portion to the south was severely degraded by clearcutting, with some areas converted to subsistence agriculture. Encroachment and degradation accelerated during the 1970s and 1980s (Hamilton 1984; Howard 1991). Landsat imagery from the mid-1980s shows most of the eastern and south-western areas to be almost entirely cleared. In 1988–89, the government evicted settlers: since then Mabira has been recovering, managed in a largely non-interventional manner.

Mabira Forest is now composed of a mosaic of patches which had been disturbed during different time periods. While encroachment has decreased in the last two decades, timber extraction continues (Baranga 2007; New Vision 2012) though the quantities extracted are poorly known. Legal extraction occurs in the eastern part on land previously heavily encroached. Mature timber trees are illegally felled elsewhere in the forest, while smaller poles are extracted for building and charcoal production, medicinal plants are harvested and Hibiscus spp. cut for cooking use.
These activities are largely focussed around the village enclaves in the forest.

Field methods

From description and maps in Howard (1991) and Davenport et al. (1996), supplemented by visual checking of Landsat imagery, we identified three types of areas of Mabira Forest with different disturbance histories; (1) Logging pre-1950 (categorised as older growth forest type), (2) Logging since 1950 (categorised as mid-secondary forest type) and (3) recovering from agricultural clearance during the 1980s (categorised as younger secondary forest type).

Plots of 10 m × 30 m were established in four to five compartments of each of the three types (Figure 1), not adjacent to large settlements and not anywhere where recent logging activity was evident. To encompass environmental variability associated with topography, plots were arranged in “triplets” of increasing distance upslope from forest streams, at 5, 65 and 125 m, with the long axis of the plots parallel to the slope. Ferns and environmental variables were sampled at all three distances between February and May 2009. Angiosperm sampling plots were situated in the same locations (subject to 10 m GPS-derived relocation error) as the 5 and 125 m plots for the ferns (but not 65 m plots, hence they formed “pairs”), and sampled in August–September 2011. Sixty-three plots in 21 triplets were sampled for ferns (12 older growth, 33 mid-secondary and 21 younger secondary) and 35 for angiosperms (four older growth, 17 mid-secondary and 14 younger secondary).

In plots where angiosperms were sampled, trees of diameter at breast height (DBH) greater than 10 cm were identified and counted across the whole plot. Ground layer vegetation up to 2 m height was sampled by dividing the 10 m × 30 m plot into 12 5 m × 5 m subplots and sampling six of these, moving along the plot on alternate sides. All
the species in these subplots were recorded, (including all woody plants large enough to identify and with stems less than 10 cm DBH; most tree seedlings below 50 cm height remained unidentified), and their percent cover estimated. Ferns were recorded in all plots, by abundance of individual stems or tufts for rhizomatous plants and individual rosettes for rosette-forming plants (Sharpe and Mehltreter 2010), estimated in classes (<5, 6–15, 16–30, 31–50, 50–100, >100). Plants which could not be identified in the field were collected and taken to Makerere University Herbarium for identification.

Environmental variables

We recorded three groups of variables which we expected to be related to the growing environment: topographical (slope and distance from stream), structural (tree basal area, leaf litter percent cover, leaf litter depth, shrub percent cover, deadwood, stumps, canopy openness) and soil (pH, carbon, nitrogen and total cations). Basal area was recorded by using a prism tally of trees with a DBH > 10 cm at the start, centre and end of each plot. Leaf litter percent ground cover was visually estimated in six 1 m × 1 m subplots, placed along the centre line of each plot at 5, 10, 15, 20, 25 and 30 m. Leaf litter depth was measured with a metal ruler to the nearest 0.5 cm in the centre of the leaf litter subplots. Shrub cover was visually estimated in the same subplots as the percent of the ground covered by a vertical projection of the shrub canopy. Deadwood was recorded as the number of deadwood items within the plot with diameter more than 25 cm and more than 1 m long. Stumps were counted in the whole area of the plot. Canopy hemispherical photographs were taken at four points along the middle line of the plot (at 0, 10, 20 and 30 m), with the lens placed at 70 cm height (Opteka HD+ 0.20X Professional Super AF Fisheye Lens for Nikon D40). Canopy percent cover was estimated from the photographs with CAN-eye software (Baret and Weiss 2004).

Five soil samples were taken from each plot (equal-sized samples to 15 cm depth, at points on the centre-line 5, 10, 15, 20 and 25 m from the shorter edge of the plot nearest our access point) and then mixed to form one composite soil sample. Soil physical and chemical properties were analysed following Okalebo et al. (1993). pH was analysed in 1:2.5 water, using a Mettler Toledo benchtop pH meter. Total nitrogen (N) was determined by the Kjeldahl method and available phosphorus (P) by absorption spectrophotometry. Total organic carbon was determined by adding potassium dichromate and concentrated sulphuric acid to 0.1 g of soil. After complete oxidation, unused dichromate was titrated against ferrous sulphate. Calcium (Ca), sodium (Na), magnesium (Mg) and potassium (K) were extracted by 1 M ammonium acetate and determined by flame photometry. Total cations were calculated as the sum of these cations. One datum point was missing from the Na dataset; as Na had little influence on total cations, the mean for Na was used for that sample.

Data analyses

The angiosperm data from the six 5 m × 5 m subplots per plot were divided into three groups: subcanopy woody plants (incorporating tree seedlings, saplings less than 10 cm DBH and shrubs), climbers, and herbs (the last group incorporating all non-woody angiosperm species including three grass species). The data from the six subplots of each plot were merged for species richness calculations, and averaged for analyses of composition. Ferns had been recorded in abundance classes, so the midpoint of the abundance class was used for statistical analyses, such that species recorded as class “<5” were assigned a nominal abundance of 2, class 6–15 was assigned 11, and so on, with class “<100” assigned 150. Tree abundance data were analysed in untransformed format.

Individuals that could not be accurately identified were removed from the dataset, except where identification was to genus and there were no other records from that genus. Unidentified species accounted for 7% of occurrences. Several taxa of climbers were recorded (28 identified, five unidentified), but because of difficulties identifying young plants, coupled with low occurrence (98 observations) and total cover (mean of 1%), these were not analysed. Species were classified according to their “usual” Ugandan habitat as forest specialists (reported only from forests), forest generalists (reported from forests and other habitats) and open habitat specialists using Davenport et al. (1996) or the Flora of Tropical East Africa (RBG Kew and East Africa Herbarium 1952–2012) for species not in Davenport et al. (1996). Summarised data for each forest type are presented in Supplementary tables (Table S1).

All analyses were carried out in R version 2.15.3 (R Core Team 2013), using the packages “vegan” (Oksanen et al. 2013) and “indicspecies” (De Cáceres and Legendre 2009). We carried out pair-wise Pearson correlations of plot-scale species richness between different species groups, to test whether plots with high species richness for one species group had high richness for other groups. We explored species cover/abundance and richness patterns between forest types using ANOVA for plot-scale data, with square-root transformation of cover data to satisfy conditions of homoscedasticity (checked by Levene’s tests). The affiliation of species to a particular forest type or combination of types was tested using point-biserial correlations (“multipatt” function in the “indicspecies” package; De Cáceres and Legendre 2009) followed by a Benjamini and Hochberg (1995) test for multiple comparisons. To test whether sites were consistently similar or dissimilar to one another across the species groups (which would suggest similar responses to environmental and land-use history variation), we compared the arrangement of samples in ordination space using Procrustes rotation of CA (correspondence analysis) ordinations (Peres-Neto and Jackson 2001). For the 25 plots with data on all four species groups, CA ordinations were generated using consistent settings (species occurring
only once in the dataset were removed to reduce noise and a square-root transform was used for cover data; Oksanen et al. 2013). The arrangement of the samples in each CA ordination space was compared using the function “protest” in the “vegan” package (Oksanen et al. 2013), with 9999 permutations.

To determine the extent of the influence of forest type on species composition, CCA analyses with step-wise selection of variables (using the function “ordistep”, with combined forward and backward selection, in the “vegan” package; Oksanen et al. 2013) were used with the same settings as the CA analyses above. Rather than using a full CCA model including all variables as a starting point, we began with the three environmental variable groups in three separate models: topographical (slope and distance from stream), structural (basal area, leaf litter cover, leaf litter depth, deadwood, stumps, canopy openness and shrub cover although this was not used in the subcanopy woody model) and soil (pH, carbon, nitrogen and total cations). For each group, step-wise selection was used and the significant variables retained. Then each retained variable, plus forest type, was included in a final model for that species group. Multicollinearity between selected variables was checked by using variance inflation factors (“vif” function, Oksanen et al. 2013); all were <5, indicating that multicollinearity was not a problem.

Species composition
Following a correction for multiple tests, no species were significantly associated with any particular forest type. The proportion of forest specialist to forest generalist species was similar across the forest types for each species group (Figure 3; trees $\chi^2 = 0.794, P = 0.672$; subcanopy woody $\chi^2 = 0.319, P = 0.853$; herbs $\chi^2 = 2.032, P = 0.362$, $\chi^2 = 0.804, P = 0.669$).

The arrangement of sites in ordination space was not significantly correlated between any of the groups; correlations ranged from extremely weak (ferns vs. herbs: rho = 0.085, $P = 0.977$) to approaching significance (herbs vs. subcanopy woody: rho = 0.409, $P = 0.095$). We note that strong (rho > 0.5) or significant ($P < 0.05$) correlations did not occur regardless of alternative settings used for the underlying ordinations (with or without removal of singletons, with or without standardisation, or use of a PCA instead of a CA; results not shown).

The species composition of the large trees was related to forest type and total soil cations (Table 1). Total soil cations were dominated (55–90%) by calcium.

However, only a small percentage of variation in species composition could be explained by soil cations once the variation related to forest type had been partitioned out (Table 1). The species composition of the subcanopy woody plants was related to forest type, total cations and leaf litter depth (Figure 4; Table 1), with most of the variation being linked to forest type alone or to the combined effects of forest type with soil cations, with little remaining variation explained by soil cations alone. The species composition of the herb flora was significantly related to forest type and leaf litter cover (Figure 4; Table 1). The species composition of the ferns was related to forest type, soil pH and slope (Figure 4; Table 1). For the herbs and ferns, the proportion of the variation explained by forest type was lower than that explained by other environmental variables. Soil nutrient values were highest in younger secondary stands (Figure S2). In addition, basal area and deadwood were significantly higher in older growth stands, but neither of these variables were found significant in the constrained ordination analyses.

Discussion
Broad plant functional groups present in Mabira Forest responded to the disturbance and subsequent period of recovery, but in different ways and hence no one plant group can predict the status of recovery of another group. Plot-scale species richness was only significantly higher in older growth forest for trees, and abundance only showed a consistent pattern for subcanopy woody plants, which had high cover values in the young secondary forest. For all groups, plant species composition was influenced by forest disturbance history, though as predicted the influence of forest type compared to other
environmental variables was lower for ferns and higher for large trees. Neither successional stage nor environmental variables explained more than 20% of the variance of any of the plant assemblages we analysed. Since the environmental and successional gradients were somewhat weak, it is not surprising that no congruence was found between groups. Trees are most often the focus of forest plant surveys (de Andrade et al. 2014) and were part of the basis for selecting Mabira as a forest reserve alongside birds and butterflies (Howard et al. 2000). However, according to our results, they should not be used alone to monitor plant biodiversity in Afrotropical forests during restoration or to select which areas to focus resources on. Instead, several taxa should be combined, according to the taxonomic expertise available locally (Kessler et al. 2011).

All groups were affected by forest type, but groups with short life cycles (herbs and ferns) were most strongly influenced by local environmental influence. This contrasts with a similar study in Guineo–Congolian semi-deciduous rainforest where tree species composition was least affected by logging compared with saplings and herbs (Decocq et al. 2014). The forest type-related differences did not lead to species of any group being classified as specialist old-growth plants, despite the fact that part of the patterns in species composition were attributed to the disturbance gradient, potentially as only a handful of species from each group occurred more than 10 times which
limits the utility of species as habitat indicators (Dufrêne and Legendre 1997).

**Influence of environment and disturbance on the different groups**

As predicted, large trees had the greatest proportion of variation explained by forest type as compared with other variables. Both growth stages of trees were affected by forest type, reflecting earlier findings from Mabira by Kirika et al. (2010). Woody species composition was also related to total soil cations, which affect woody composition of tropical forests at the seedling establishment stage (Holste et al. 2011), during growth and at dieback (Dezzeo et al. 1997; Baker et al. 2003). Soil cations and forest type were related, with higher concentrations of soil cations in the younger secondary forest. The subcanopy woody species were most abundant in younger secondary forest, while large trees were slightly less abundant in young secondary forest. Additionally, some species present as saplings were not present among the mature trees; species accumulation curves suggest that this is not due to undersampling of the trees compared to the subcanopy woody plants (data not shown). This suggests that either filtering effects occur in the transition from saplings to trees, for example, based on soil nutrients (Paoli et al. 2006; Comita and Hubbell 2009), or that recovery is ongoing and some tree species will become part of the canopy at a later stage of succession.

Leaf litter cover was the strongest determining environmental variable for herbs, as could be expected as a gap in the litter cover is required for the relatively small seeds of herbs to germinate and become established (Fowler 1988; Uriarte et al. 2010). Many herb species colonised the younger secondary forest, so there are probably adequate dispersal opportunities (either temporal or spatial), but the relative role of seed bank and seed rain in forest herb establishment depends on gap characteristics and seed production as well as the presence of effective dispersal mechanisms (Castillo and Stevenson 2010).

Fern species composition was the least influenced by forest type among the groups we analysed, though the influence of the local environment on fern species composition was also not strong. Our interpretation of these results is that either the ferns are more affected by variables we did not measure (e.g. soil moisture), or their distribution is influenced more by chance dispersal events (Hubbell 2001; Hubbell 2001). However, half the fern species were found in all forest types and other evidence suggests ferns are generally well dispersed at this scale (Soltis and Soltis 1990; Flinn 2007). As ferns were the only group which had a topographical variable, slope, selected in the CCA, our expectation that microhabitat is important is supported to
some extent: the undulating topography and high rainfall of Mabira means that streams and rivers run through the valleys and so conditions on the steeper valley sides are expected to be relatively moist. Additionally, steeper slopes lead to more open forest floor, increasing germination opportunities (de Oliveira Rodrigues and Costa 2012). Leaf litter depth is negatively correlated with slope in Mabira (data not shown) and came closest of all the structural variables in the ordination analyses to being a significant explanatory factor of fern composition.

The recovery of Mabira forest from disturbance

Afrotropical forests in particular have a long history of disturbance (Tovar et al. 2014), so a baseline or “pristine” condition is not present and cannot be used as the target for Mabira. Also, keystone animal species, especially large herbivores and carnivores, have not returned and are unlikely to do so given the strong human imprint on the landscape surrounding Mabira.

Since protection in 1990, the younger secondary forest has recovered enough to have a closed canopy and we recorded only one “open habitat” species (Habenaria geniculata), though this forest type still has a high cover of shrubs and saplings and there remain clear differences in composition between the forest types for all species groups. Unlike several examples from elsewhere (e.g. Benitez-Malvido and Martinez-Ramos 2003; Von Oheimb and Härdtle 2009), the older-growth stands in Mabira do not contain a particularly high proportion of

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Figure 4. Constrained ordination (CCA) plots for plant species groups recorded in Mabira Forest, with point colour indicating forest type. The contour lines illustrate the most important environmental variable as indicated by selection modelling; contours displayed here were fitted as generalised additive models for single variables. The CCAs were constrained as follows: Large (>10 cm DBH) tree species: forest type and soil total cations – Total cations fitted as a contour. Eigenvalues are 0.41 for axis 1 and 0.28 for axis 2. Tree seedlings, saplings (>10 cm DBH) and shrub species (altogether classed as “subcanopy woody”) – forest type, leaf litter depth and soil total cations. Total cations (milliequivalents) fitted as a contour. Eigenvalues are 0.26 for axis 1 and 0.17 for axis 2. Herbs – forest type and leaf litter cover. Log (leaf litter percent cover) fitted as a contour. Eigenvalues are 0.34 for axis 1 and 0.31 for axis 2. Ferns – forest type, slope and soil pH. Soil pH fitted as a contour. Eigenvalues are 0.43 for axis 1 and 0.37 for axis 2.
In contrast with forests in the south-west of Uganda, regeneration in Mabira has not been arrested by the invasive shrub *Lantana camara* (Totland et al. 2005; Safari and Byarugaba 2008; Omeja et al. 2011); no *L. camara* was recorded in our plots, but it grows in gaps elsewhere in Mabira (Totland et al. 2005). Other non-native species were recorded in our survey. In particular, the paper mulberry *Broussonetia papyrifera* is abundant in the younger secondary forest (up to 14 mature individuals per plot with seedlings making 25% cover) but does not persist in the older stages. *Broussonetia papyrifera* can reduce the cover of indigenous species (Bosu et al. 2013), but some young secondary stands containing the species had high species richness in the subcanopy woody group (Figure 2a).

All of the tree species present in the mature trees were present also among the subcanopy woody plants, suggesting that natural regeneration is taking place. Forest specialist species have reappeared in all forest types but do not increase with time since disturbance, so it is unclear whether some strongly disturbance-sensitive species are “missing” entirely from our dataset, or that the recovery is well underway across all types of forest. Among the large trees are several species considered late-successional, but also several pioneer species (according to Lwanga 2003).

There are no quantitative data for Mabira from before commercial exploitation and the disturbance history of African forests goes back far beyond our temporal gradient (Willis et al. 2004). Besides this, ongoing climatic and environmental changes imply that past community composition is no longer a useful reference state (Tylianakis et al. 2008; Gardner et al. 2009). Without a clear “endpoint” for recovery, it may be that further research efforts should be focussed on ensuring adequate functional diversity in Mabira—a challenge given the relative scarcity of functional trait data for African species. So far, the reinstatement of continuous canopy over large areas that were clear-felled can be seen as successful “passive” restoration, and so forest management in Mabira should most likely continue to focus on preventing logging and encroachment (Chazdon et al. 2009; Laurance et al. 2012).

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None of the authors have any conflict of interest to declare.
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Supplemental data
Supplemental data for this article can be accessed here.

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