

North American tree migration paced by fecundity
and recruitment through contrasting mechanisms east
and west

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Abstract

Global forest diebacks are the beginnings of change that will be controlled by tree migration, which combines two uncertain processes, tree fecundity and recruitment. Knowledge of how, and where, tree migration can proceed is critical for adaptive management of forest resources and conservation efforts. The initial stage of seed production is erratic and poorly observed, with most studies limited to few trees, few species and few sites. At the next stage, tree recruitment is typically too sporadic to characterize at landscape scales. Neither seed production nor seedling recruitment have been quantified or linked to climate and habitat variables at scales needed to evaluate the changes happening now or to anticipate the diversity and structure of 21st century forests. As part of the masting inference and forecasting (MASTIF) project, we synthesized continental-scale data for tree fecundity gathered over the last half century and combined it with forest inventories to connect adult trees (basal area) to i) fecundity (seeds per basal area) and ii) recruitment (recruits per seed). A dynamic model fitted to $> 10^7$ tree years of fecundity data provided estimates tree-by-year fecundity. A predictive distribution for the continent combines the fitted mode with 10^5 trees from Forest Inventory Analysis (FIA), Canadian National Forest Inventory (CNFI) and the National Ecological Observatory Network (NEON).

Results show continent-wide migration as a balance between regional shifts in fecundity that can diverge from conditions that favour establishment, with clear differences in eastern and western North America. In moist eastern states, the geographic centers for fecundity are most commonly displaced south of tree basal area for the same species. This relationship would be expected if optimal conditions for seed production lie to the south of optimal conditions for growth and survival, despite potential benefits of warming poleward. In the dry west and north-central, for some species fecundity is displaced northwest of tree basal area, as would be expected if the high-rainfall northwest is predisposed to lead migration as the continent warms. The east-west contrast diminishes at the transition from fecundity to recruits per seed, which tends to be shifted north in both regions. The net continent-wide migration by contrasting east-west controls highlight interactions, with fecundity primed to lead tree migration in the west, and fecundity slowing progress in the east. The possibility of fecundity limitation offers one explanation for migration lag in species expected to track climate warming by expanding poleward.

Introduction

The recent increases in tree mortality rates have been well documented globally for a variety of forest ecosystems (van Mantgem et al., 2009, Wigneron et al., 2020, Millar and Stephenson 2015, Schwantes et al., 2016). These forest dieback events are indicative of a change that will be controlled by tree migration. The critical signal for migration in trees comes from a shift of juveniles poleward of basal area (Zhu et al., 2014), and therefore involves two uncertain processes; fecundity and recruitment. To this end, we present an analysis that links predictions of fecundity to estimates of recruitment and abundance for 65 tree species across North America. We find two emerging patterns for the relationships between fecundity, recruitment and basal area: first, a pattern indicating a northward migration of the species where the favourable conditions for recruitment and fecundity are both north of basal area, and second, where favourable conditions for fecundity are located south of tree basal area and favourable conditions for recruitment north of basal area. The latter pattern may suggest a possible lag in migration of tree species towards higher latitudes, despite climate warming. Overall, we suggest that in order to anticipate the structure, diversity and distribution of forests under a changing climate, the complex mechanisms of migration at the species level must be evaluated.

There has been ongoing debate as to whether species are tracking climate warming and expanding into northern ranges (Woodall et al., 2008, Zhu et al., 2011, Chen et al., 2008). For trees, evidence of potential latitudinal range shifts is mostly based on the observation of temporal changes in spatial distribution of occurrence or abundance patterns (Boisvert-Marsh et al., 2014, Fei et al., 2017, Zhu et al., 2011, Sittaro et al., 2017). Evidence suggests that conditions for optimum forest growth have shifted in recent decades across elevation gradients (Feeley et al., 2011) and latitudes (Fei et al., 2017). While the epicenter of abundance indicates present day optimal growth conditions, shifts in the epicenter cannot be interpreted as migration because the connection of growth or abundance to new recruitment is highly indirect. The migration or persistence of a tree species under climate change will ultimately depend on the biogeography of successful regeneration (Bell et al., 2014) and so relates directly to fecundity and recruitment. The ability of a tree species to colonize new environments under climate change will be facilitated or limited by the conditions for fecundity and recruitment (Veresoglou and Halley 2018, Ibanez et al., 2008,2009, Clark 1998, Morin et al., 2007, Clark et al., 2011).

Despite it's importance, clear evidence of latitudinal changes in tree species distribution is still limited (Boisvert-Marsh et al., 2014). Insufficient data coverage and poor/imprecise survey methodology confounds broad-scale assessment of tree shifts (Woodall et al. 2009, Tingley and Beissinger 2009). Seed production has been studied

over relatively small scales (Koenig et al., 1999, Liebhold et al., 2004) and concentrated at the species level (Koenig et al., 1999, Lamontagne and Boutin, 2007, Dale et al., 2001). Further, seed production has not been linked to tree abundance, climate and habitat variables on scales needed to evaluate migration potential of forests. At the next stage, studies that have compared the biogeography of adult trees and saplings have yielded contradictory patterns depending on the species or the portion of range examined (Woodall et al., 2009, 2013, Zhu et al., 2011, 2014, Boisvert-Marsh et al., 2016). Such analyses also do not shed light on how fecundity may affect the migratory response of forests to climate change. Overall, in the absence of continent wide fecundity and recruitment estimates, the inference on tree migration at broad-scales has been inconclusive.

Here we synthesize continental-scale data for tree fecundity gathered over the last half century as a part of the Masting Inference and Forecasting (MASTIF) project and combine forest inventories to provide the first opportunity to connect adult trees (basal area) to fecundity (seeds per basal area) to recruitment (recruits per seed). The shift of recruitment poleward of basal area is a sign of migration (Zhu et al., 2011) however the critical indicator for migration comes from linking tree basal area, fecundity and recruitment. For example, is optimal fecundity shifting relative to recruitment and basal area? If so, is a poleward shift in optimal fecundity leading or trailing shifts in recruitment? We consider two hypotheses for the relationships between tree basal area, fecundity and recruitment that affect migration and the interpretation of data. We acknowledge that there is a lack of prior evidence for the relationship between tree abundance, recruitment and fecundity, and therefore cannot comment on the spatio-temporal change in optimal conditions for fecundity and recruitment.

Hypothesis 1: Convergent response

Recruitment responds to climatic changes in the same way as fecundity, shifting the center for recruitment in the same direction as that of fecundity, relative to basal area (figure 1a). This would occur if optimal fecundity and juveniles were both tracking conditions towards the same direction. For example, if fecundity is more sensitive than growth to change in growing season length, then the geographic center for optimal fecundity may be poleward of basal area. If recruitment follows the direction of fecundity relative to basal area, this may be treated as the sign of migration in that direction.

Hypothesis 2: Recruitment overcompensation

In the second case, the direction of response for fecundity and recruitment are divergent (figure 1b). This would occur if fecundity and recruitment are tracking different conditions i.e., if different life stages have different niche requirements (Chase and Leibold, 2003). For example, if fecundity is more sensitive than growth to water limitations, the center of mass for fecundity might be shifted south of tree basal area. On the other

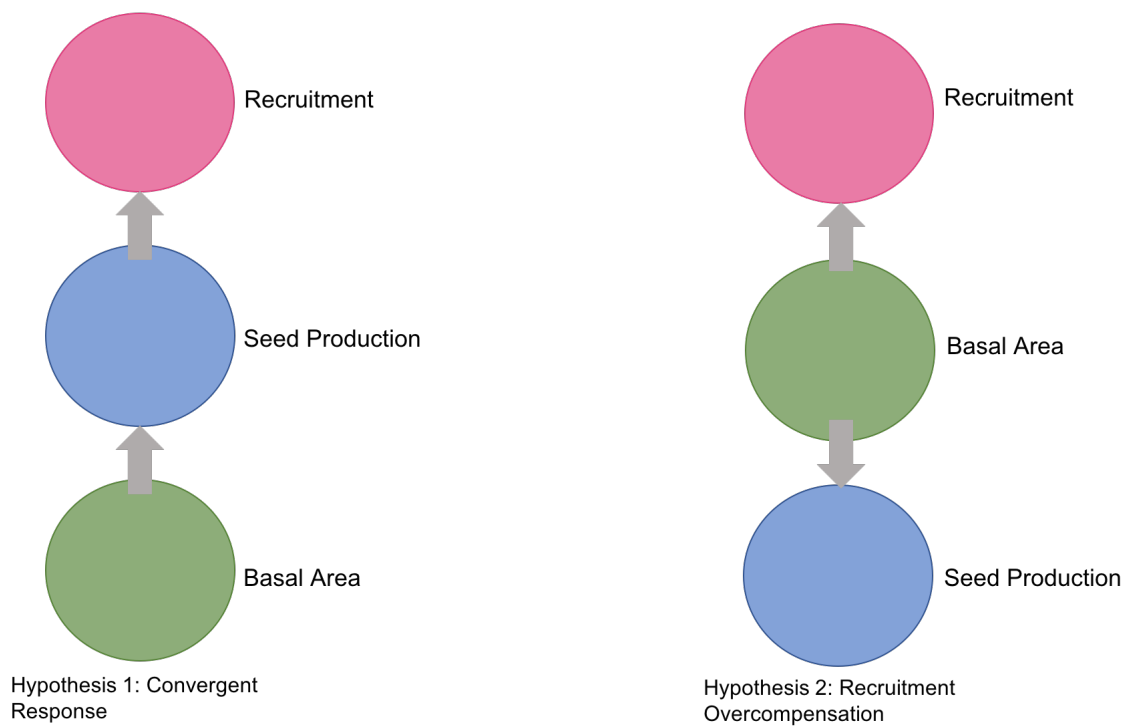


Figure 1: Illustrative figure of Hypotheses 1 and 2. Each circle represents the centers of a life stage (adult trees, seeds or recruits). These centroids may be interpreted as the current optimum conditions for that life stage. While the optimum conditions for different life stages are unexpected to coincide, Hypothesis 1 indicates that the displacement between optimum growth, seed production and recruitment are in the same direction. Hypothesis 2 represents the idea that the optimum conditions for seed production and recruitment are in opposing directions. The direction of the arrows do not correspond to a geographic direction

hand, if recruitment is tracking the warming temperature towards higher latitudes, the centroid for recruitment will be moved north of basal area. Therefore, fecundity and recruitment will have divergent responses to changing climates. In this case, recruitment is overcompensating for lagging fecundity at the northern edges of the species range.

Methods

To link fecundity to recruitment and basal area at the continent-scale, we synthesized and combined data from the MASTIF Network, Forest Inventory Analysis (FIA), Canadian National Forest Inventory (CNFI) and National Ecological Observatory Network (NEON) inventories. The seed production data from longstanding plots part MASTIF long-term monitoring network span the continent. MASTIF has more than 500 plots and crop-count locations. The plots cover a wide range of climates and ecoregions including sites in Great Smoky Mountains, Harvard forest, California montane woodlands, Central Rockies forests, South-east conifer forests and so on. The dataset holds over 9×10^6 data points from seed traps for over 800 species from 100 families (for more details, refer to Clark et al., 2019). Abundance or basal area was estimated using diameter at breast height (d.b.h) measurements from longstanding plots of the FIA, CNFI and NEON. Recruitment was recorded as in-growth into these long standing plots (the minimum diameter at which recruitment is recorded is ~ 3 inches).

To connect fecundity to basal area and recruitment on the same spatial scale, we modelled fecundity using crop counts and seed trap data using the MASTIF R Package (Clark et al., 2019). Predictors of fecundity include individual traits, climate variables such as spring minimum temperature ($^{\circ}\text{C}$) and thermal surplus (cm/month), synchronicity with other trees are lag effects. For model fitting, we include species observed in multiple years with at least 10 individuals. We fitted and studied patterns for 65 tree species. The model fitted to $\geq 10^7$ tree years provided a posterior distribution that seamlessly connects to a predictive distribution implemented for $\geq 10^5$ trees from inventories of FIA, CNFI, NEON and MASTIF. Seed production estimates per species were predicted on the same spatial grid as obtained for basal area of trees and recruitment. Inference was performed on individual tree years, and therefore is consistent with the scale at which climate change operates.

To analyze relative positions of favourable conditions for fecundity, basal area and recruitment, we computed the geographic centroid for each variable as,

$$\bar{X} = \frac{\sum_{i=1}^n w_i X_i}{\sum_{i=1}^n w_i}, \bar{Y} = \frac{\sum_{i=1}^n w_i Y_i}{\sum_{i=1}^n w_i}$$

where (\bar{X}, \bar{Y}) are the mean latitudes and longitudes for abundance/recruitment/fecundity weighted geographic centers. X_i and Y_i are the latitudes and longitudes for each plot and w_i the value of the variable at the plot. The weighted geographic centers are interpreted as the positions for favourable conditions for growth, recruitment or fecundity.

Results

When examining the relationships between fecundity, recruitment and basal area, we find two patterns emerge. The first is a northward displacement of optimal fecundity and recruitment relative to growth (described in Hypothesis 1: Convergent Response). Species such as *Tsuga mertensiana*, *Thuja plicata*, *Abies alba*, *Abies fraseri*, *Pinus virginia* among others exhibit this pattern. The second pattern is a northward displacement of recruitment relative to basal area but southward displacement of fecundity, as described by Hypothesis 2: Recruitment Overcompensation. Species exhibiting this pattern include *Carya alba*, *Carya texana*, *Quercus agrifolia*, *Picea rubens* among others. Most of the species exhibiting this pattern are eastern species.

The east-west contrast disappears at the transition from seeds to recruits per seed (figure 2b). Recruitment is predominantly located north of fecundity for western and north eastern species. A different pattern emerges in the south east, where favourable conditions for recruitment are located south of fecundity centers. At the final stage, we find that recruitment is leading northward migration for species in the west and parts of the east. Strikingly, there are considerable shifts east/west rather than north/south. Continent-wide recruitment is leading both tree basal area and seed production, including that conditions for germination and/or seedling establishment are responding even faster than fecundity. The majority of the species are undergoing migration at the continental scale. The net effect of stage transitions is shown in figure 2c. In the west, fecundity is primed to lead tree migration, whereas in the east, it commonly lags behind recruitment. Therefore in the west, the major pattern followed by species is that expected from Hypothesis 1, where fecundity and recruitment are moving in the same direction relative to tree basal area. In the east, the pattern followed by the a considerable number of species is from Hypothesis 2, where fecundity and recruitment have divergent responses relative to basal area. For many eastern species, recruitment overcompensates the lag of fecundity in the northern range of species.

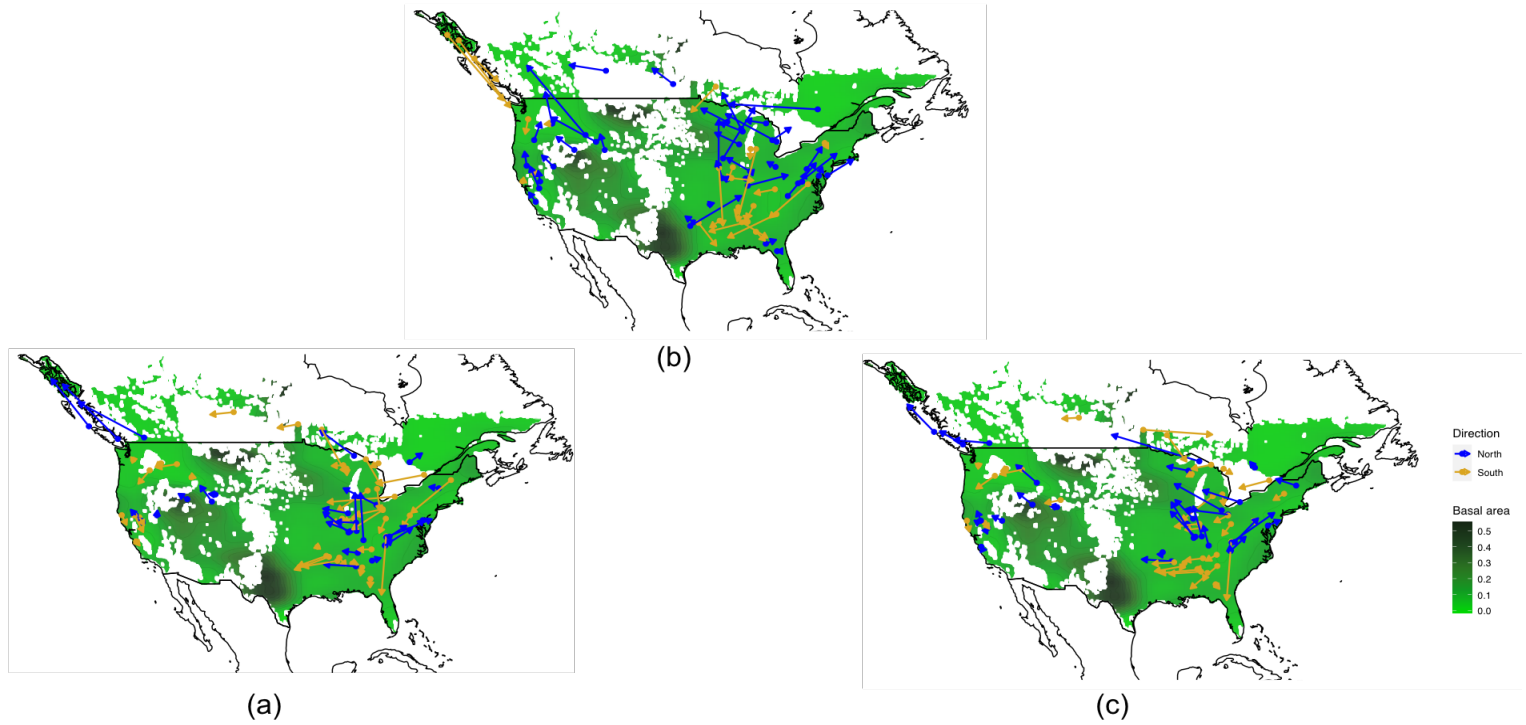


Figure 2: Each species modelled in this study is represented by a dot. In (a) the points correspond to the tree abundance centroids per species and arrows are drawn to fecundity centroids for that species. The arrows are coloured blue for northward shifts and orange for southward shifts, (b) each points represents the centroid of fecundity and arrows are drawn to recruitment centroids and finally (c) represents net migration across the continent. Each point is basal area for a species and arrows are drawn to the species' recruitment centroid.

The east-west contrast for fecundity relative to basal area is explored further in Figure 3. In terms of direction, there is a clear shift south and southwestward for tree species present in the east, with exceptions moving north and east. The magnitude of the displacement of fecundity relative to basal area is varied, with species such as *Pinus strobus*, *Magnolia acuminata*, *Picea rubens*, *Betula alleghaniensis* among others, with the largest displacements southward. A handful of species in the east have northward displaced fecundity- *Pinus virginia*, *Quercus coccinea*, *Quercus montana*, among others. The overall northward displacement of fecundity is outweighed by the a southward and westward displacement. In the west, there is a more tempered response. Some species present in the west have east and southeast displaced fecundity. However, the largest displacement is seen in species moving northwest.

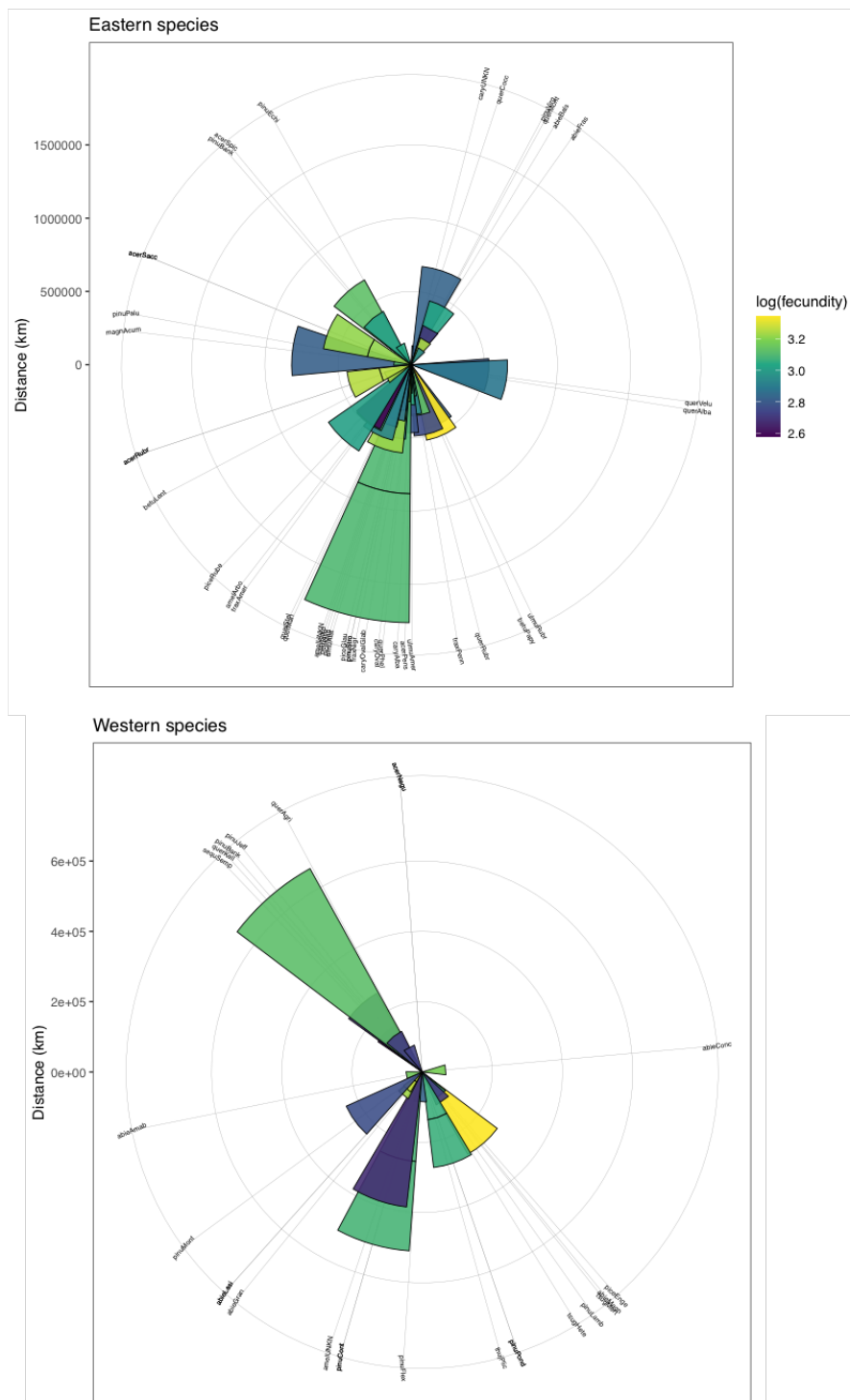


Figure 3: Each vector in these diagrams represents the direction and distance from the center of mass of tree basal area to the center of mass for fecundity. The direction corresponds to a cardinal direction, going clockwise from North to South. The length of each vector is the distance between basal area and fecundity centroids. Each vector is coloured by the logarithm of it's seed production estimate (seeds per m² per year). The diagrams are split by Eastern (top) and Western species (bottom). There are some species that appear in both diagrams such as *Acer negundo*.

Discussion

The spatio-temporal distribution of a population ultimately arises from the rates at which individuals grow, reproduce, disperse and die (Pulliam 2000, Schurr et al., 2012). Studies analysing the migration of tree species have focused on observed spatio-temporal changes in the relative positions of juveniles to adults (Woodwall et al., 2008, Zhu et al., 2014, Bosivert-Marsh, 2016, Sittaro et al., 2017). In this study, for the first time, we introduce fecundity to understand in detail the relative positions of optimal conditions for all life stages relevant to migration.

For the transition from tree basal area to fecundity we found an east-west contrast. In the moist eastern North America, a majority of species show a strong tendency for optimal fecundity shifted well south or west of tree basal area (figure 2a). A contrasting northward displacement of fecundity arises in the west. Notably, on average, the distance of displacement in the west is greater in the east, possibly signalling a larger shift.

The east-west contrast in fecundity relative to tree basal area is striking. The development of moisture limitation over successive years appears to be particularly important for fecundity (Clark et al., 1998) The result of this is species in the moist eastern regions exhibit a fundamentally different pattern from the dry west (figure 2a). The dominant equator-ward shift in fecundity in east is consistent with temperature limitation where moisture is abundant. Contrasting northward displacement of fecundity in the west suggests predominant moisture limitation and optimal fecundity that could already be leading pole ward migration out ahead of tree basal area. In fact, arrows in the West point northwest (figure 2a), indicating fecundity displaced toward not only north but also toward the moist Pacific Northwest.

The FIA and CNFI datasets have been used extensively in examining range shifts in species distributions across large geographic scales (Woodall et al., 2008, 2013, Murphy et al., 2010, Zhu et al., 2011, 2014, Nock et al., 2013, Monleon and Lintz 2015). The results yielded from these studies are often contradictory. A number of studies indicated that North American tree species are undergoing range expansion at the northern edge due to greater regeneration success at higher latitudes (Murphy et al., 2010, Woodall et al., 2008). However, results from Zhu et al., (2011) report a failure to migrate, suggesting a limited range expansion or stability at the northern range edge as well as a contraction at the southern range limit for tree species in the eastern United States. Fei et al., (2017) found a shift in abundance over a 30 years period where tree species, including at low latitudes, were moving westward, tracking moisture.

From our analysis, it is clear that continent wide migration is taking place. The migration pattern in this analysis indicates not only a northward movement of species, but also a westward move. This is expected due to increased warming and regeneration success at higher latitudes (Woodall et al., 2008, Sittaro et al., 2017). Further, the westward move is in line with the results from Fei et al. (2017), possibly suggesting that species are tracking moisture in addition to temperature.

This analysis offers one explanation for the migration lag reported by studies (Zhu et al., 2011, Sittaro et al., 2017). A key piece comes from the comparison between the center of mass for recruitment relative to fecundity. For a significant number of species, recruitment is located north of fecundity indicating that populations in the northern ranges may be limited by fecundity. As fecundity lags behind, recruitment is overcompensating for the northward movement of populations. For example, Sittaro et al., (2017) reports species such as *Tilia americana*, *Pinus strobus* and *Acer rubrum* fail to expand northward in pace with climate warming. The center of mass of fecundity relative to basal area for each of these species is located southward (figure 3). The possibility of fecundity limitation offers one explanation as to why there might be a lag in migration for many species expected to track climate warming and expand their northern ranges. For species exhibiting the Recruitment Overcompensation pattern, as favourable conditions for fecundity of these species is located south of recruitment, the northward migration of the species is possibly limited by fecundity.

Conclusion

With recent climate change, forest ecosystems are likely to reorganize and redistribute. Part of this response is controlled by tree migration which itself is led of two processes- fecundity and recruitment. The migration of trees ultimately depends on the biogeography of it's successful regeneration. This analysis presents the first opportunity to connect fecundity to recruitment to basal area on a continent-wide scale. There are two primary patterns to emerge from our analysis- a case where fecundity is leading the northward migration of tree species (described by Hypothesis 1: Convergent Response) and a case where fecundity is limiting the northward migration of species (described by Hypothesis 2: Recruitment Overcompensation). In the second case, the northward migration of species is led by recruitment but offers on explanation as to why some species may fail to migrate to keep pace with climate warming in higher latitudes. The results from our study indicate that fecundity is either leading or limiting the northward migration of tree species in North America.

References

- [Beckage and Clark, 2003] Beckage, B. and Clark, J. S. (2003). Seeding survival and growth of three forest tree species: the role of spatial heterogeneity. *Ecology*, 84(7):1849–1861.
- [Bell et al., 2014a] Bell, D. M., Bradford, J. B., and Lauenroth, W. K. (2014a). Early indicators of change: divergent climate envelopes between tree life stages imply range shifts in the western united states. *Global Ecology and Biogeography*, 23(2):168–180.
- [Bell et al., 2014b] Bell, D. M., Bradford, J. B., and Lauenroth, W. K. (2014b). Mountain landscapes offer few opportunities for high-elevation tree species migration. *Glob Chang Biol*, 20(5):1441–51.
- [Bertrand et al., 2011] Bertrand, R., Gégout, J.-C., and Bontemps, J.-D. (2011). Niches of temperate tree species converge towards nutrient-richer conditions over ontogeny. *Oikos*, 120(10):1479–1488.
- [Boisvert-Marsh et al., 2014] Boisvert-Marsh, L., Périé, C., and de Blois, S. (2014). Shifting with climate? evidence for recent changes in tree species distribution at high latitudes. *Ecosphere*, 5(7).
- [Boisvert-Marsh et al., 2019] Boisvert-Marsh, L., Périé, C., de Blois, S., and Bellingham, P. (2019). Divergent responses to climate change and disturbance drive recruitment patterns underlying latitudinal shifts of tree species. *Journal of Ecology*, 107(4):1956–1969.
- [Buotte et al., 2019] Buotte, P. C., Levis, S., Law, B. E., Hudiburg, T. W., Rupp, D. E., and Kent, J. J. (2019). Near-future forest vulnerability to drought and fire varies across the western united states. *Glob Chang Biol*, 25(1):290–303.
- [Chisholm et al., 2014] Chisholm, R. A., Condit, R., Rahman, K. A., Baker, P. J., Bunyavejchewin, S., Chen, Y. Y., Chuyong, G., Dattaraja, H. S., Davies, S., Ewango, C. E., Gunatilleke, C. V., Nimal Gunatilleke, I. A., Hubbell, S., Kenfack, D., Kiratiprayoon, S., Lin, Y., Makana, J. R., Pongpattananurak, N., Pulla, S., Punchi-Manage, R., Sukumar, R., Su, S. H., Sun, I. F., Suresh, H. S., Tan, S., Thomas, D., and Yap, S. (2014). Temporal variability of forest communities: empirical estimates of population change in 4000 tree species. *Ecol Lett*, 17(7):855–65.
- [Clark, 1998] Clark, J. S. (1998). Why trees migrate so fast: confronting theory with dispersal biology and the paleorecord. *The American Naturalist*, 152(2):204–224.

- [Clark et al., 2011] Clark, J. S., Bell, D. M., Hersh, M. H., and Nichols, L. (2011). Climate change vulnerability of forest biodiversity: climate and competition tracking of demographic rates. *Global Change Biology*, 17(5):1834–1849.
- [Clark et al., 2014] Clark, J. S., Bell, D. M., Kwit, M. C., and Zhu, K. (2014). Competition-interaction landscapes for the joint response of forests to climate change. *Glob Chang Biol*, 20(6):1979–91.
- [Clark et al., 2016] Clark, J. S., Iverson, L., Woodall, C. W., Allen, C. D., Bell, D. M., Bragg, D. C., D’Amato, A. W., Davis, F. W., Hersh, M. H., Ibanez, I., Jackson, S. T., Matthews, S., Pederson, N., Peters, M., Schwartz, M. W., Waring, K. M., and Zimmermann, N. E. (2016). The impacts of increasing drought on forest dynamics, structure, and biodiversity in the united states. *Glob Chang Biol*, 22(7):2329–52.
- [Copenhaver-Parry et al., 2019] Copenhaver-Parry, P. E., Carroll, C. J. W., Martin, P. H., Talluto, M. V., and Morueta-Holme, N. (2019). Multi-scale integration of tree recruitment and range dynamics in a changing climate. *Global Ecology and Biogeography*, 29(1):102–116.
- [Feeley et al., 2012] Feeley, K. J., Rehm, E. M., and Machovina, B. (2012). perspective: The responses of tropical forest species to global climate change: acclimate, adapt, migrate, or go extinct? *Frontiers of Biogeography*, 4(2).
- [Feeley et al., 2011] Feeley, K. J., Silman, M. R., Bush, M. B., Farfan, W., Cabrera, K. G., Malhi, Y., Meir, P., Revilla, N. S., Quisiyupanqui, M. N. R., and Saatchi, S. (2011). Upslope migration of andean trees. *Journal of Biogeography*, 38(4):783–791.
- [Hendrik Davi and Fady, 2016] Hendrik Davi, Maxime Cailleret, G. R. A. A. C. P. and Fady, B. (2016). Disentangling the factors driving tree reproduction. *Ecosphere*, 7(9):1–16.
- [HilleRisLambers and Janneke, 2015] HilleRisLambers, S. J. K. and Janneke (2015). Recruitment limitation of long-lived conifers: implications for climate change responses. *Ecology*, 96(5):1286–1297.
- [I-Ching Chen and Thomas, 2011] I-Ching Chen, Jane K. Hill, R. O. D. B. R. and Thomas, C. D. (2011). Rapid range shifts of species associated with high levels of climate warming. *Science*, 333(6045):1024–1026.
- [Ibanez et al., 2009] Ibanez, I., Clark, J. S., and Dietze, M. C. (2009). Estimating colonization potential of migrant tree species. *Global Change Biology*, 15(5):1173–1188.

- [Inez Ibanez and Lambers, 2007a] Inez Ibanez, James S. Clark, S. L. and Lambers, J. H. R. (2007a). Exploiting temporal variability to understand tree recruitment response to climate change. *Ecological Monographs*, 77(2):163–177.
- [Inez Ibanez and Lambers, 2007b] Inez Ibanez, James S. Clark, S. L. and Lambers, J. H. R. (2007b). Exploiting temporal variability to understand tree recruitment response to climate change. *Ecological Monographs*, 77(2):163–177.
- [Iverson and McKenzie, 2013] Iverson, L. R. and McKenzie, D. (2013). Tree-species range shifts in a changing climate: detecting, modeling, assisting. *Landscape Ecology*, 28(5):879–889.
- [J. Lenoir and Brisse, 2008] J. Lenoir, J.C. Gegout, P. M. P. d. R. and Brisse, H. (2008). A significant upward shift in plant species optimum elevation during the 20th century. *Science*, 320(5884):1768–1771.
- [Jason S. McLachlan and Manos, 2005] Jason S. McLachlan, J. S. C. and Manos, P. S. (2005). Molecular indicator of tree migration capacity under rapid climate change. *Ecology*, 86(6):2088–2098.
- [Kelly and Gouliden, 2008] Kelly, A. E. and Gouliden, M. L. (2008). Rapid shifts in plant distribution with recent climate change. *Proc Natl Acad Sci U S A*, 105(33):11823–6.
- [Koenig, 2002] Koenig, W. D. (2002). Global patterns of environmental synchrony and the moran effect. *Ecography*, 25:283–288.
- [Lazarus and McGill, 2014] Lazarus, E. D. and McGill, B. J. (2014). Pushing the pace of tree species migration. *PLoS One*, 9(8):e105380.
- [McDowell et al., 2015] McDowell, N. G., Coops, N. C., Beck, P. S., Chambers, J. Q., Gangodagamage, C., Hicke, J. A., Huang, C. Y., Kennedy, R., Krofcheck, D. J., Litvak, M., Meddens, A. J., Muss, J., Negrón-Juárez, R., Peng, C., Schwantes, A. M., Swenson, J. J., Vernon, L. J., Williams, A. P., Xu, C., Zhao, M., Running, S. W., and Allen, C. D. (2015). Global satellite monitoring of climate-induced vegetation disturbances. *Trends Plant Sci*, 20(2):114–23.
- [Perie and de Blois, 2016] Perie, C. and de Blois, S. (2016). Dominant forest tree species are potentially vulnerable to climate change over large portions of their range even at high latitudes. *PeerJ*, 4:e2218.
- [Phillip J. van Mantgem, 2009] Phillip J. van Mantgem, Nathan L. Stephenon, J. C. B. (2009). Widespread increase of tree mortality rates in the western united states. *Science*, 323(5913):521–524.

- [Rogers et al., 2017] Rogers, B. M., Jantz, P., and Goetz, S. J. (2017). Vulnerability of eastern us tree species to climate change. *Glob Chang Biol*, 23(8):3302–3320.
- [Schwantes et al., 2016] Schwantes, A. M., Swenson, J. J., and Jackson, R. B. (2016). Quantifying drought-induced tree mortality in the open canopy woodlands of central texas. *Remote Sensing of Environment*, 181:54–64.
- [Sittaro et al., 2017] Sittaro, F., Paquette, A., Messier, C., and Nock, C. A. (2017). Tree range expansion in eastern north america fails to keep pace with climate warming at northern range limits. *Glob Chang Biol*, 23(8):3292–3301.
- [Songling Fei, 2017] Songling Fei, Johanna M. Desprez, K. M. P. I. J. J. A. K. C. M. O. (2017). Divergence of species responses to climate change. *Science Advances*, 3(5):e1603055.
- [Stephenson and L., 2015] Stephenson, C. I. M. and L., N. (2015). Temperate forest health in an era of emerging megadisturbance. *Science*, 349(6250):823–826.
- [Woodall et al., 2009] Woodall, C. W., Oswalt, C. M., Westfall, J. A., Perry, C. H., Nelson, M. D., and Finley, A. O. (2009). An indicator of tree migration in forests of the eastern united states. *Forest Ecology and Management*, 257(5):1434–1444.
- [Zhu, 2014] Zhu, K. (2014). Climate change and forest biodiversity in the eastern united states: Insights from inventory data. *Duke Dissertation*.
- [Zhu et al., 2011] Zhu, K., Woodall, C. W., and Clark, J. S. (2011). Failure to migrate: lack of tree range expansion in response to climate change. *Global Change Biology*, 18(3):1042–1052.
- [Zhu et al., 2014] Zhu, K., Woodall, C. W., Ghosh, S., Gelfand, A. E., and Clark, J. S. (2014). Dual impacts of climate change: forest migration and turnover through life history. *Glob Chang Biol*, 20(1):251–64.