THE ROLE OF LAMIN ASSOCIATED DOMAINS IN GLOBAL CHROMATIN ORGANIZATION AND NUCLEAR ARCHITECTURE

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A dissertation submitted to The Johns Hopkins University in conformity with the requirements for the degree of Doctor of Philosophy

Baltimore, Maryland
March 2016

ABSTRACT

Nuclear structure and scaffolding have been implicated in expression and regulation of the genome (Elcock and Bridger 2010; Fedorova and Zink 2008; Ferrai et al. 2010; Li and Reinberg 2011; Austin and Bellini 2010). Discrete domains of chromatin exist within the nuclear volume, and are suggested to be organized by patterns of gene activity (Zhao, Bodnar, and Spector 2009). The nuclear periphery, which consists of the inner nuclear membrane and associated proteins, forms a sub-nuclear compartment that is mostly associated with transcriptionally repressed chromatin and low gene expression (Guelen et al. 2008). Previous studies from our lab and others have shown that repositioning genes to the nuclear periphery is sufficient to induce transcriptional repression (K L Reddy et al. 2008; Finlan et al. 2008). In addition, a number of studies have provided evidence that many tissue types, including muscle, brain and blood, use the nuclear periphery as a compartment during development to regulate expression of lineage specific genes (Meister et al. 2010; Szczerbal, Foster, and Bridger 2009; Yao et al. 2011; Kosak et al. 2002; Peric-Hupkes et al. 2010). These large regions of chromatin that come in molecular contact with the nuclear periphery are called Lamin Associated Domains (LADs).

The studies described in this dissertation have furthered our understanding of maintenance and establishment of LADs as well as the relationship of LADs with the epigenome and other factors that influence three-dimensional chromatin structure. I provide evidence that LAD patterns from DNA adenine methyltransferase identification (DamID)-derived molecular contact maps are reflective of higher order chromatin structure in both ensemble population measure

and single cells. Importantly, this work provides the first *in situ* visualization of chromosome-wide molecular data in a single cell. These data, showing LAD and nonLAD organization, indicate that there is a speicifc and reproducible organization of sub-chromosomal domains. In addition, this work has furthered our understanding of the influence of chromatin state on both LAD and overall chromosome organization—demonstrating that higher-order chromatin structure and epigenetic signatures are closely linked. This work has contributed to the finding that LAD formation can be sequence driven, which was uncovered by examining variable LADs (vLADs) where LAD patterning differs between cell types. Also, examination of LADs across multiple cell types has uncovered genomic characteristics that can define LADs and may have a functional role in the process of genome organization

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ACKNOWLEDGEMENTS

I would like to express my gratitude to Dr. Karen Reddy for accepting me into her lab and granting me her guidance, support, and patience throughout my doctoral work. Karen has provided me a great opportunity to train as a scientist on a project that is both meaningful and exciting, while also taking a sincere interest in fostering my professional and personal strengths. I am grateful to have worked with Karen throughout my graduate degree and know I will always be able to reflect on my time with her when searching for direction in years to come.

Thank you to all the faculty who have provided insight and encouragement during my Ph.D. work. Thank you Drs. Sean Taverna, Jef Boeke, Xin Chen for serving on my thesis committee and your support and suggestions. A special thank you to Sean for his humor and constant support, and for working with me to complete this dissertation. Thank you Drs. Barbara Sollner-Webb and Kathy Wilson, who along with Karen have led by example and shared their opinions on how to succeed as a woman in science. Thank you to Dr. Carolyn Machamer for helping us navigate the path to graduation, especially in the final stages of my degree. Also, thank you to Drs. Trina Schroer, Andy Hoyt, Joel Schildbach, who were key players in my decision to pursue a doctoral research degree

I also wish to recognize our generous collaborators Drs. Roger Reeves, Andy Feinberg, and especially Agilent Technologies and Dr. Alice Yamada who provided the novel LAD and nonLAD sub-chromosome paints. Their material contributions and guidance were critical to the success of this project.

I must thank my colleagues in the lab and the Epigenetics Center for their skills, advice, and friendship. Specifically I would like to thank all the members of the Reddy lab Drs. Xianrong Wong, Marie-Cecile Gaillard and Jennifer Harr, Mohammad Heydarian and Jevon Cutler, for their scientific collaboration during my graduate work. I would especially like to thank Jevon Cutler and Dr. Xianrong Wong for their friendship in the lab, which has been crucial for my personal and professional well-being. I especially want to thank my colleagues from the Epigenetics Center who have doubled as very close friends, Bridget O'Brien, Carolina Montano, and Drs Romeo Papazyan, Annie Cieniewicz, and Tonya Gilbert for all the fun, love, and support without which I would not have made it through.

Thank you to the Federation of American Societies for Experimental Biology and the Office of Public Affairs where I spent a three month internship working on science policy and Congressional affairs, for the opportunity to expand my scientific world-view beyond the bench, and develop my professional skills. The experience was invaluable and I hope to continue to advocate for science throughout my career. Specifically, I would like to thank Dr. Howard Garrison and Dr. Anne Deschamps for the opportunity to work in the office and their continued guidance and friendship.

I want to thank my personal support team, my friends and family, for encouraging me to never give up. Thank you Rachel Cylus and Dr. Kate Szarama for standing by me regardless of the time or distance between us. Thank you to all my family members who cheered me on and always met me with love and kindness. I would especially like to thank my parents Angela and Domenic Romeo, and my siblings Francesca Romeo and Frank Romeo for their unwavering support. I would like to thank my grandmothers Francesca Dattola and Teresa Romeo, who I miss very much, for their love, and for knowing they would be very proud of me.

Lastly, I give the biggest thank you to my amazing husband Dan and sweet daughter Clara. You both are my everything and I would be nothing without you. Thank you for loving me and never letting go.

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CHAPTER 1: INTRODUCTION

1.1 Epigenetics and Chromatin

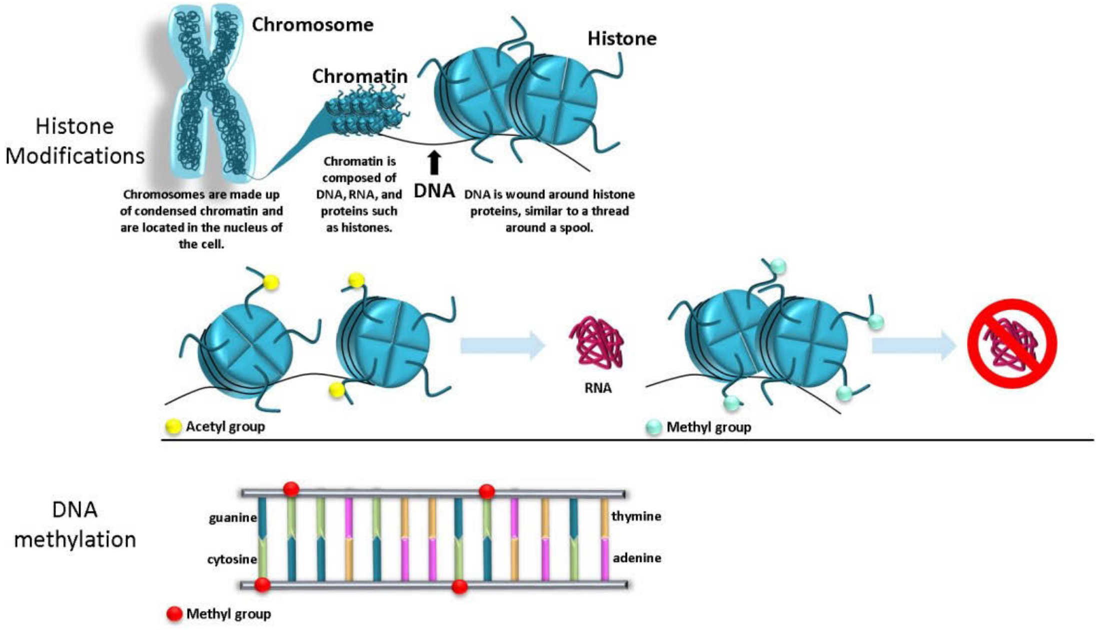
Our DNA, the genetic code that defines our existence passed from mother and father, is present in each of the 37.2 trillion cells in our body. The DNA sequence of Gs, As, Ts, and Cs is the same from cell to cell, but each cell type behaves uniquely. These differences are heritable through cell division and do not involve changes to the underlying DNA sequence. This 'epigenetic' regulation affects how the genes are expressed in a cell-type specific manner, partially explaining how different cells in metazoans, which all house the same DNA, display very unique phenotypes and gene expression patterns. These differences are manifest throughout development and are crucial to the function of the diverse cell types that make up a multi-cellular organism. Epigenetic changes are the result of differences in the network of proteins, protein modifications, regulatory RNAs, DNA methylation and nuclear structure and organization, and its complexity is not yet fully understood. Disruptions of the epigenome can result in disease and examination of epigenetic pathways will lead to discovery and can identify potential targets for therapy.

In eukaryotic cells, DNA is highly organized within the nucleus. DNA is condensed into chromatin, packaged into chromosomes and then bundled into the nucleus. The nucleosome is the fundamental subunit of chromatin, consisting of 146 base pairs of DNA wrapped around a core histone octamer (a single octamer consists of a tetramer of histones H3 and H4 and two histone H2A:H2B dimers) (Luger et al. 1997). Nucleosomes along with histone H1 linkers are further packaged into higher order chromatin structures. (Figure1) These structures (DNA plus histones with associated proteins and complexes) serve as the substrate for virtually all nuclear events (transcription, replication, recombination, and repair) and are, therefore, highly and dynamically regulated. Nuclear organization is manifest in the arrangement of this chromatin into domains of gene activity and compaction (heterochromatin and euchromatin), chromosome territories and into sub-chromosomal organizational domains, such as lamina associated domains (LADs) and topologically associated domains (TADs), among others (Comings 1980; Cremer and Cremer January; Guelen et al. 2008; Nora et al. 2012; Dixon et al. 2012).. Some of these architectural domains, such as heterochromatin, found in and around centromeres, near the nucleolus, and at the nuclear periphery, can be observed by simply using a light microscope and a DNA counterstain (Heitz 1929; Boveri 1914).

Figure 1 Mechanisms of Epigenetics.

Histone modifications contribute to gene control and transcription. Activating marks such as acetylation promote RNA transcripts while certain types of histone methylation are related to shut down of active transcription (Top). DNA methylation is associated with gene silencing (Bottom).

Adapted from art by Anne Deschamps, FASEB Horizons in Bioscience

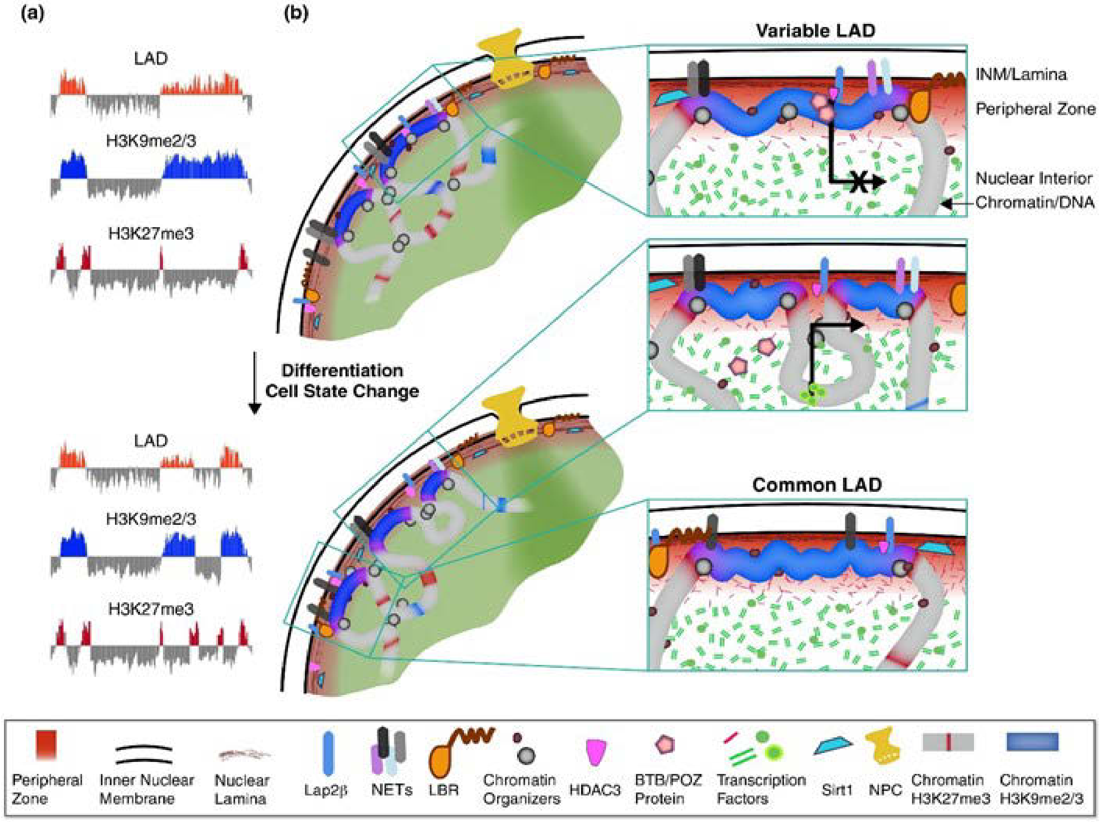


At the molecular level, heterochromatin contains histones with specific ‘silencing’ post translational modifications (PTMs) on the tails of histones and has been shown to be (generally) more densely packed and transcriptionally ‘silent’ for protein coding genes (Kouzarides 2007). For example, constitutive heterochromatin often harbors histone H3 lysine 9 trimethylation (H3K9me3) and facultative heterochromatin can be enriched in histone H3 lysine 9 dimethylation, histone H3 lysine 27 trimethylation and histone H4 lysine 20 di- and trimethylation (H3K9me2, H3K27me3 and H4K20me2/3, respectively)(Kouzarides 2007). Euchromatic regions of open, transcriptionally active regions of chromatin often carry histone PTMs such as acetylation on numerous H3 and H4 lysine residues as well as histone H3 lysine 4 trimethylation (H3K4me3) (Kouzarides 2007a). In addition to local modifications and chromatin compaction, DNA is organized and regulated by other factors including non-coding RNAs, insulator proteins, and associations with nuclear bodies and structures. More recently, genome-wide and cytological studies have pointed to a role for distinct nuclear compartments that are enriched in regulatory or structural proteins in both higher level genome organization and gene regulation (reviewed in Mao, Zhang, and Spector 2011). The nuclear periphery is one such compartment that has been implicated in and studied as a scaffold for genome organization and as a regulator of development and disease.

1.2 Nuclear Structure and the Nuclear Periphery

Figure 2 Components of the Peripheral Zone

Chromatin association with the nuclear periphery and scaffolding in the peripheral zone is cell type specific and dynamic through differentiation. The Nuclear lamina and peripheral zone facilitate gene regulation during differentiation and cell state changes through genome organization. Specifically, modifications and LAD profiles change during differentiation or cell state change (top To bottom nucleus). LAD,H3K9me2/3 (LOCK) And H3K27me3 Molecular profiles of chromatin depicted in each nucleus are represented in panel A. (b) cLAD regions remain at the periphery before and after cell state change (bottom inset), variable LADs move to or away from peripheral zone (red shaded region near nuclear lamina) and may be accompanied by gene activation or repression (top insets, shown to move away, with gene activation). Once at the periphery, LAD regions are retained in the peripheral zone (but are away from nuclear pore complexes — NPC in gold) and are generally overlapped by H3K9me2/3 domains (blue shading). Edges of LADs have H3K27me3 marks (red) and border regions contain both H3K27me2/3 and H3K27me3 (purple shading). H3K27me3 exists throughout the genome outside of LAD and LAD border regions (red). Proteins in the nuclear lamina and inner nuclear membrane are presumably involved in establishment of the peripheral zone (lamin A/C, lamin B1, NETs, LBR, Lap2 b , Sirt1) as well as transcription factors (green and red factors throughout nuclear interior). Chromatin insulators (such as CTCF) are found both at boundaries of LADs and throughout the genome to facilitate chromosome organization. Lap2β, HDAC3 and Zbtb7b (BTB-POZ protein) have been demonstrated to be involved in scaffolding vLADs. Tissue specific factors (such as TAF3 in myoblast differentiation) are able to promote transcriptional activation of genes upon dissociation of regions from the peripheral zone that is linked with developmental progression (B, vLAD insets).



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The nuclear periphery is a unique compartment comprised of a repertoire of INM proteins and the underlying nuclear lamina. This lamina meshwork, composed of the nuclear coiled-coil domain proteins lamin A/C and B type, serves as retention/docking sites for the INM proteins and interfaces with the nuclear envelope and chromatin (Gruenbaum et al. 2005).. Specifically, there are at least 60 unique nuclear envelope (NE) proteins that contribute to the complexity of the nuclear lamina network, including INM proteins such as Lamin B Receptor (LBR), Lamina associated peptide 2 (Lap2 also known as thymopoietin or TMPO) and Emerin (EMD) (Wilson and Berk 2010). These and other NE proteins, including proteins extending into the cytoplasm (e. g. the SUN and KASH domain proteins), interact with the nuclear lamina. In addition to other roles, many of the INM proteins, such as LBR, Emerin, and Lap2, are also able to interact with transcriptional repressors, chromatin modifiers and core histones (Zullo et al. 2012; Guarda et al. 2009; Ye et al. 1997; Haraguchi et al. 2004; Holaska et al. 2003). This results in a unique compartment at the nuclear periphery. The nuclear lamina network has been implicated directly in genome organization, epigenetic modulation and gene regulation, likely impacting both developmental and disease progression.

Early electron-microscopy data shows an obvious enrichment of heterochromatin at the edge of the nucleus, a region we define as the ‘peripheral zone’ (Figure2) (Luperchio, Wong, and Reddy 2014). These regions of chromatin that come in contact with the nuclear lamina are called ‘lamina associating domains’, or LADs. Sequences comprising LADs are identified by the DamID technique (an in depth description is provided in Chapter 2), which results in genome-wide maps of chromatin contacts at the nuclear periphery. Initial reports characterizing LADs described them as large

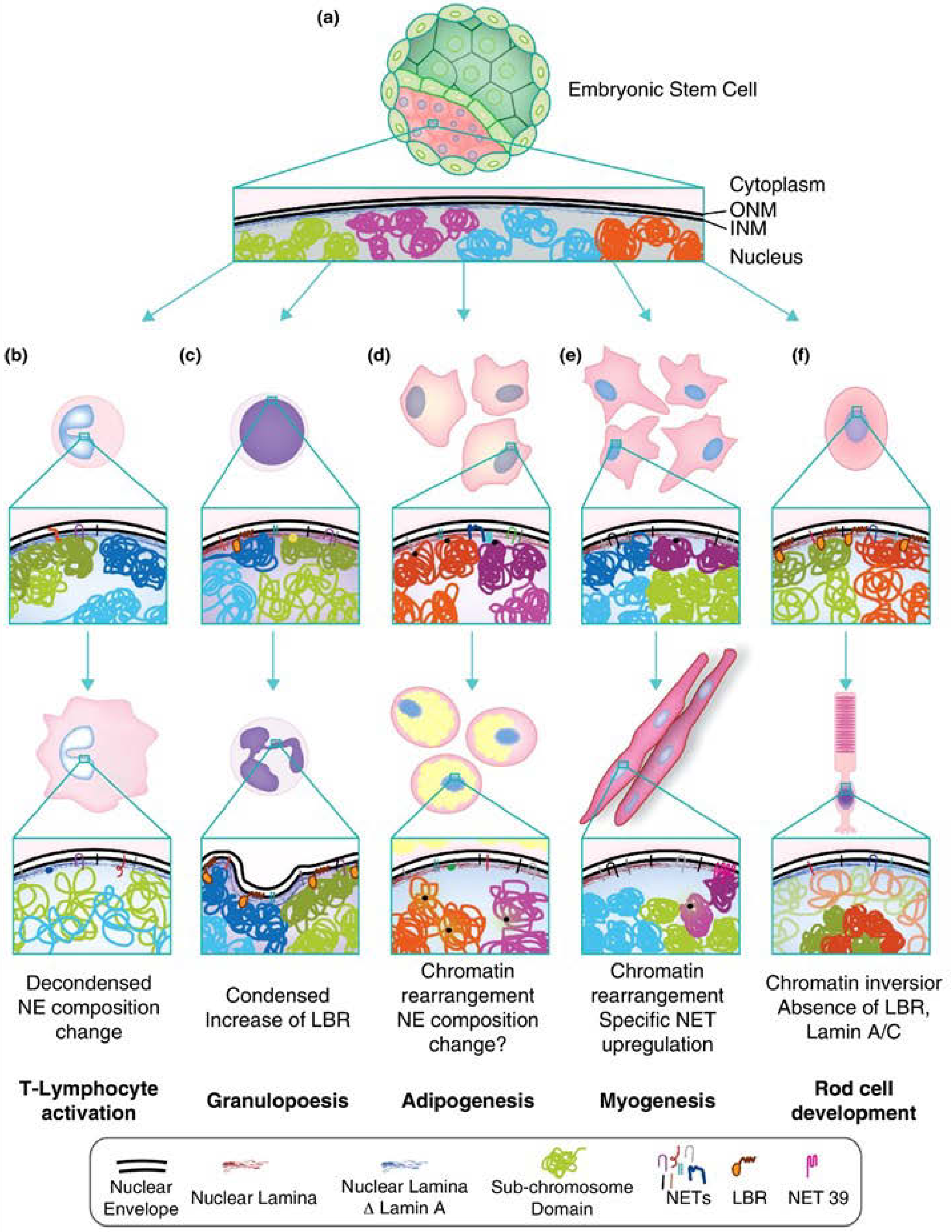
(0.1-10Mb) silent domains and gene 'deserts' (Guelen et al. 2008). A natural hypothesis from the cytological observations of these domains is that LADs will overlap canonical epigenetic characteristics of heterochromatin. While it is difficult indeed to show such enrichment by cytological methods, the associations become more clear by bioinformatically comparing genome-wide chromatin immunoprecipitation (ChIP) followed by massively parallel deep sequencing (ChIP-seq) data with profiles of DamID identified LADs (DamID-array and DamID-seq). We and others have noted (described further in Chapters 4 and 5) that LAD borders, but not the interior of these domains, are enriched in the facultative heterochromatin histone H3 lysine 27 trimethylation (H3K27me3, Figure 2a) (Guelen et al. 2008; Harr et al. 2015; Zullo et al. 2012; Luperchio, Wong, and Reddy 2014). Interestingly, similar ChIP experiments for the histone H3 lysine 9 di- or tri-methylation (H3K9me2/3) modification shows a domain profile similar to LAD in size, distribution and position (Figure 2a) (Wen et al. 2009). When these large organized chromatin (H3 lysine 9) K9 modifications (LOCKs) were compared to available LAD data, an approximate 80% overlap was noted. However, these assays were done in disparate cell types. In the same cell type, it is clear that the relationship between LADs and LOCKs are very closely linked, but not absolute, discovered through work presented in later chapters here. It appears that two heterochromatin marks, H3K27me3 and H3K9me2/3 LOCKs, are correlated with LADs. Determining the dynamic and causal relationship between LADs and LOCKs, i.e. if LAD association is dependent upon chromatin state or vice versa (or both) is of interest and our work addressing this question is presented in a number of experiments throughout this dissertation. By understanding the protein composition at the nuclear periphery and the genomic/epigenetic features of chromatin that resides there, we can begin to understand the peripheral zone as a regulatory compartment for gene expression, development, and disease.

1.3 LADs in regulation

While initial studies describe LADs as silent domains devoid of genes, we and others have found that developmentally regulated genes are highly enriched in these domains when they are transcriptionally inactive, and have therefore focused our studies on the regulatory potential of LADs. (Reddy et al. 2008; Zullo et al. 2012). The nuclear periphery as a compartment for gene regulation is seen in a number of developmental programs including muscle cell, neural and lymphocytes as well as across multiple species. During differentiation there is sometimes a marked reorganization of the genome that is also cell-type specific (Figure 2b, Figure 3) reviewed in (Luperchio, Wong, and Reddy 2014; Wong, Luperchio, and Reddy 2014). Proteins at the nuclear lamina differ from cell type to cell type and these differences likely aid in the cell-type reorganization of chromatin. In many cases, developmentally regulated genes reside at the nuclear periphery while inactive, and become more centrally disposed during gene activation. We propose that this reorganization is mediated through cell type-specific modular chromatin/DNA interactors, including nuclear envelope transmembrane proteins (NETs) and other nuclear lamina associating proteins. As mentioned above, developmentally regulated genes appear to be enriched in these peripheral domains, leading to the hypothesis that LADs serve as ‘facultative’ heterochromatin domains during development (see below) (Peric-Hupkes et al. 2010; Meuleman et al. 2013). It is important to note that, while LADs mostly comprise inactive chromatin, there are several notable examples (primarily by cytology) of lamina-proximal genes being actively transcribed (Kumaran and Spector 2008; Yao et al. 2011; Brickner et al. 2012). These genes may interact with nuclear pore complexes, which have been shown to reside in a euchromatic environment, perhaps to both facilitate transcriptional activation and transport mRNA into the cytoplasm (Brickner et al. 2012). Nonetheless, it is the inactive, dynamic and gene-containing LADs that comprise an active area of research for our group to enable studies on the function of such domains both in dynamic chromosome architecture and gene regulation. Peripheral association of chromatin regions has been demonstrated to silence genes upon forced localization of ectopic genome sites to the inner nuclear membrane (Reddy et al. 2008; Finlan et al. 2008). These functional experiments are consistent with numerous genome-wide and cytological studies correlating cytological positioning of developmentally regulated loci at the lamina (Kosak et al. 2002; Szczerbal, Foster, and Bridger 2009; Williams et al. 2006; Meister et al. 2010; Zullo et al. 2012; Peric-Hupkes et al. 2010; Yao et al. 2011). Taken together these data strongly suggest a role for the nuclear periphery in the dynamic establishment and/or maintenance of gene repression and a rapidly growing focus of research is the developmentally dynamic interaction of the genome and epigenome with the nuclear lamina and the peripheral zone (Figure 1).

Figure 3 Tissue specific nuclear architecture and NETs observed during development/differentiation

Embryonic stem cells (ES cells, a), which differentiate into all cell types, have a unique nuclear architecture as determined by the chromosome conformation capture method, Hi-C. NET composition of the nuclear `. We also highlight several different cell types and subsequent nuclear architecture changes that occur upon stimulation or developmental progression. We highlight changes that occur during T cell activation (b) granulopoiesis (c) adipogenesis (d) , myogenesis (e) , and rod cell development (f) . During T-cell activation (b), the composition of the nuclear envelope changes and the activated T-cell (b, bottom) displays generally decondensed chromatin and a notable loss of heterochromatin at the nuclear periphery. During granulopoesis (c) as promyelocytes (c, top) differentiate into neutrophils (c, bottom) there is a characteristic increase in lamin B receptor (LBR) levels and a concordant decrease in lamin A, which results in increased heterochromatin at the nuclear periphery and the characteristic hyper-lobulated nuclear morphology of the neutrophil (C, bottom). Adipogenesis (fat cell differentiation, d) also demonstrates nuclear architecture changes, and a number of differentiation specific genes have been shown to move away from the nuclear periphery and into the nuclear interior upon activation (from a LAD to a non-LAD, d, bottom, genes depicted as black dots on chromatin domains). We speculate that this process is accompanied by a nuclear envelope proteome change. Myogenesis, or differentiation of myoblasts into myotubes and ultimately muscle tissue (e), also exhibits a change in the NET proteome, specifically the expression of NET39, which is important for proper positioning of chromosomes 5 and 12. MyoD , a gene encoding a key regulator of myogenesis, is also observed to assume a more central location within the myotube nucleus (black region of chromatin, e) and this movement corresponds with upregulation of MyoD . During rod cell differentiation and maturation (f) nuclear architecture dramatically changes with the displacement of heterochromatin to the center of the nucleus in an inverted conformation. This reorganization is concurrent with the loss of LBR at the nuclear periphery, in a process that appears to be the opposite of what occurs in granulopoesis (c). Each distinct cell state has a unique nuclear architecture and nuclear envelope proteome that are both important for proper development and differentiation. (Figure continued on next page)



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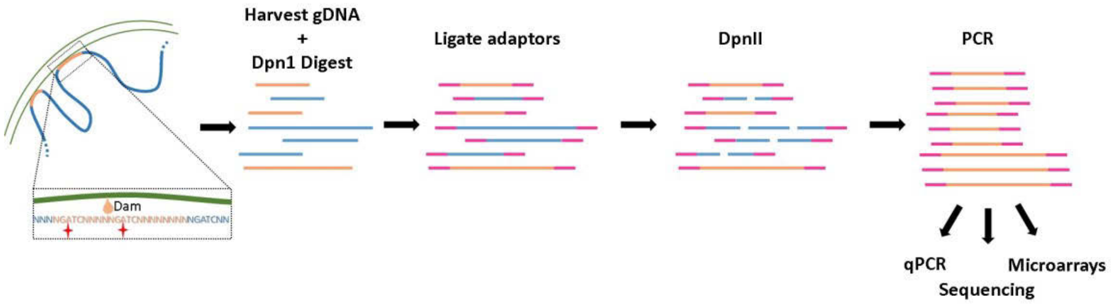
CHAPTER 2: LAD DEFINITION

2.1 Introduction

As mentioned previously, the original identification (sequence) of LADs was provided through a molecular technique to probe all chromatin contacts at the nuclear periphery called DamID.(Vogel, Peric-Hupkes, and van Steensel 2007) (Figure 4) DNA adenine methyltransferase Identification (DamID) is a technique utilizing the adenine methyltransferase enzyme from bacteria, fused to a protein (e.g. the nuclear lamin protein LaminB1 which is used in all experiments described here, unless otherwise stated), and stably introduced and expressed in higher eukaryotic cells via viral transduction. Chromatin that comes in molecular contact with the Dam protein will become methylated on adenines, a mark that is normally absent from and innocuous to higher eukaryotes. In this method, cells are virally transduced with Dam-only expressing vector as a control for freely accessible chromatin that may come in contact with the Dam methylase, and a parallel population of cells are transduced with a Dam-LaminB1 expressing vector, which localizes the Dam. This targeting of Dam to the nuclear periphery permanently marks any DNA in contact with the fusion with G^{me}ATC (Figure 4). Cells are briefly expanded then harvested for genomic DNA. The purified DNA is digested with DpnI, which cuts G^{me}ATC sequences, then the new blunt ends are ligated with double stranded DNA oligonucleotides which serve as adapters for a subsequent PCRs. After ligation, the DNA material is digested with DpnII which cuts unmethylated GATC sequences, thereby reducing long fragments that are not in contact with the periphery and reducing background (Figure 4). Post DpnII digestion, the material is amplified using an oligo complimentary to the ligated adapters to create a library of DNA segments. This material can then be quantified by qPCR, hybridized to microarray, or sequenced to gather data on enrichment of regions at the nuclear periphery (Figure 4).

Figure 4 DamID Schema

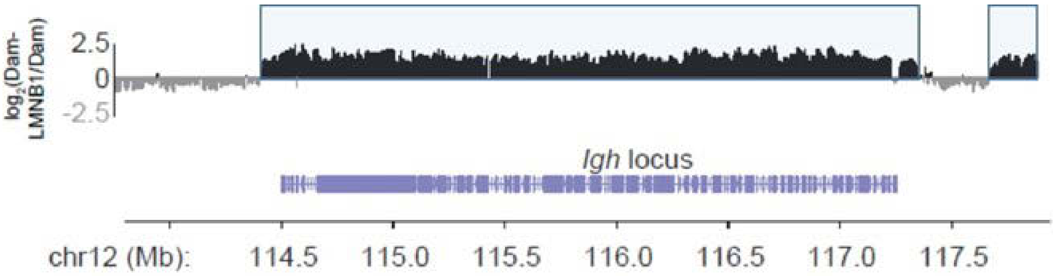
Regions of chromatin that come in contact with the nuclear periphery embedded with Dam-laminB1 protein (or any other NL protein) will accumulate methylated adenines. After exposure, genomic DNA is harvested and digested with DpnI, specifically cutting at methylated adenines. Double stranded adapters are ligated on to blunt cut ends, and then the entire population of DNA fragments are digested with DpnII to cut unmethylated GATCs and reduce background. Fragments with adapters on both ends are amplified in a ligation mediated PCR and the library can then be used in qPCR, hybridization to microarray, or DNA sequencing.



Regardless of technique used to identify individual fragments in the library, any measurements of enrichment at the nuclear periphery come from normalization of Dam-LaminB1/Dam signals. The data resulting from normalization is a $\log_2$ ratio score indicating total enrichment (Figure 5). Anything above zero is enriched in Dam-LaminB1 fragments and is considered associated with the nuclear periphery and anything at or below zero is considered not associated, or a nonLAD. Because of the permanent marking all chromatin association with the periphery including the unstable or transient associations, it is especially important to acknowledge this experimental caveat when considering interactions at the population or single cell level. Only by normalizing samples to the Dam-only control (as described in the initial DamID papers) can one exclude regions that have been marked in both target and control populations, indicating they are freely accessible to the nuclear volume.

Figure 5 Example of DamID data

Regions of LaminB1 association are defined by positive log₂ ratio signals of Dam-LaminB1/Dam. LAD regions are highlighted in blue boxes.

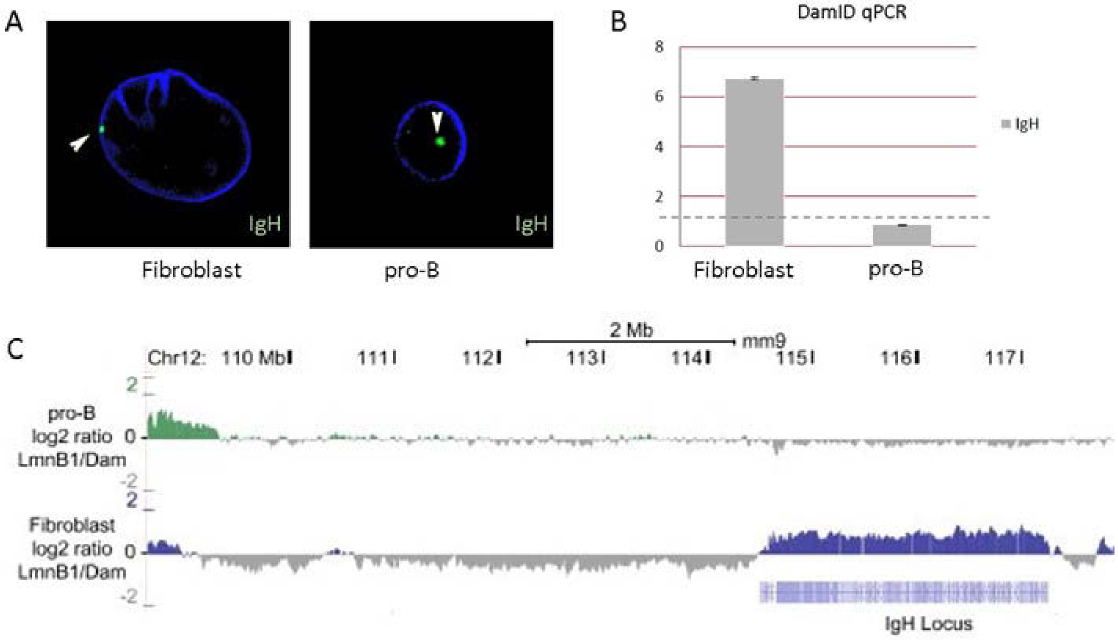


2.2 LADetector Algorithm

LADs have been defined specifically as large, 0.1-10Mb regions of chromatin that come in contact with the nuclear periphery (Guelen et al. 2008). To identify LADs from chromosome and genome-wide data, especially to determine confluence with other features such as chromatin modifications, bioinformatics approaches are necessary to determine start and end positions of LAD domains, or "call" LADs. Our initial observations of published LAD data defined by a Hiddden Markov Model (HMM) approach led us to believe that the LAD compilation was incomplete and many of the edges of the LAD domains were 'called' imprecisely. In addition, the original method for defining start and stop positions of the LADs was done on custom microarrays where data over certain genomic coordinates was missing or omitted. In order to obtain a more complete picture of LAD organization, we created a better and more precise algorithm for defining LAD start and stop locations, which we call the 'LADetector'. The LADetector is a circular binary segmentation (CBS) based approach. CBS is a recursive algorithm originally used to detect copy number variation (CNV). CNV usually results in very abrupt changes between probes/signals along the genome—a result of a discrete change in copy number. Because DamID domains display similar characteristic, we reasoned that a modification of this technique would enable robust detection of the lamina associated domains as well.

Figure 6 Validation of DamID libraries using IgH locus as a control

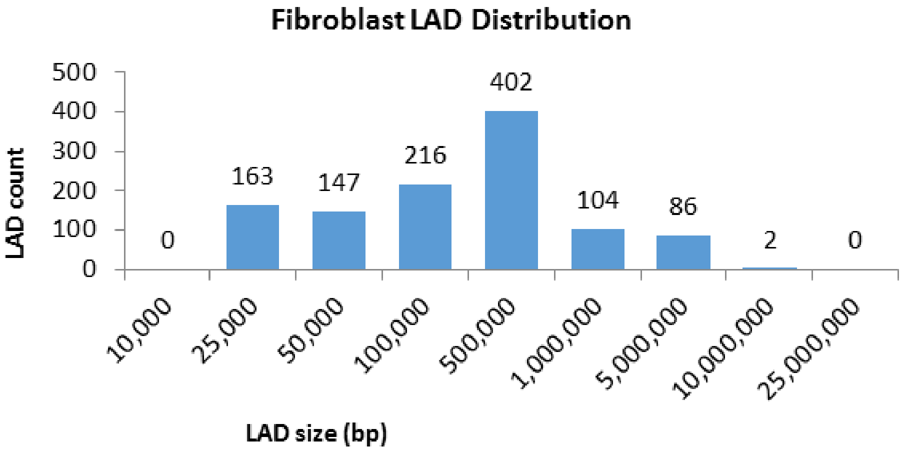
The Immunoglobulin heavy chain locus (IgH) is responsible for VDJ recombination in the B cell lineage during antibody production. The IgH locus is centrally disposed in early B cells at the pro-B cell stage of development (panel A, right) and is transcriptionally active while in other cell types such as mouse embryonic fibroblasts IgH is silenced at the nuclear periphery (panel A left.) Preparation of DamID material from fibroblasts and pro-B cells shows that Dam-LaminB1 signal is enriched at the IgH locus and pro-B does not show significant positive signal (panel B, Y axis is Dam-LaminB1 signal/Dam, dotted line indicates threshold defining positive signal. Regions of LaminB1 association are defined by positive log$_2$ *ratio signals of Dam-LaminB1/Dam in both pro-B cells and fibroblasts, where IgH shows enrichment of signal and pro-B shows a lack of signal over IgH, confirming cytological data (panel C)*



DamID was performed on two disparate cell types: Fibroblasts and pro-B cells. Our expectation was to find an enrichment of Dam-LaminB1 labeled material over the Dam-Only material at the *IgH* locus in fibroblast, but not pro-B cells, based on cytological data and previously published data (Figure 6a) (Reddy et al. 2008). As described more deeply in Chapter 3, the immunoglobulin heavy chain locus is actively recombined in B cells at the pro-B cell stage during early antibody creation, and the locus is centrally located within the nucleus of pro-B cells. In all other cell types, including MEFs, the *IgH* locus is transcriptionally silent and located at the periphery of the nucleus as observed by 3D immuno-FISH. Initial qPCR data using the *IgH* locus as a control region and detection of enrichment of Dam-LaminB1 signal over Dam-only signal in fibroblasts and not in pro-B cells indicate that DamID and creation of the library were successful (Figure 6b).

Figure 7 LAD distribution over Chromosomes 9-14 by microarray

DamID was performed in fibroblasts and the Dam-LaminB1 and Dam libraries were hybridized to two color Nimblegen arrays containing genomic coordinates of part of chromosome 9 through part of chromosome 14. Log$_2$ *ratios were plotted from the array data and the LADetector algorithm was applied to define LAD regions. LADs were binned and counted.*



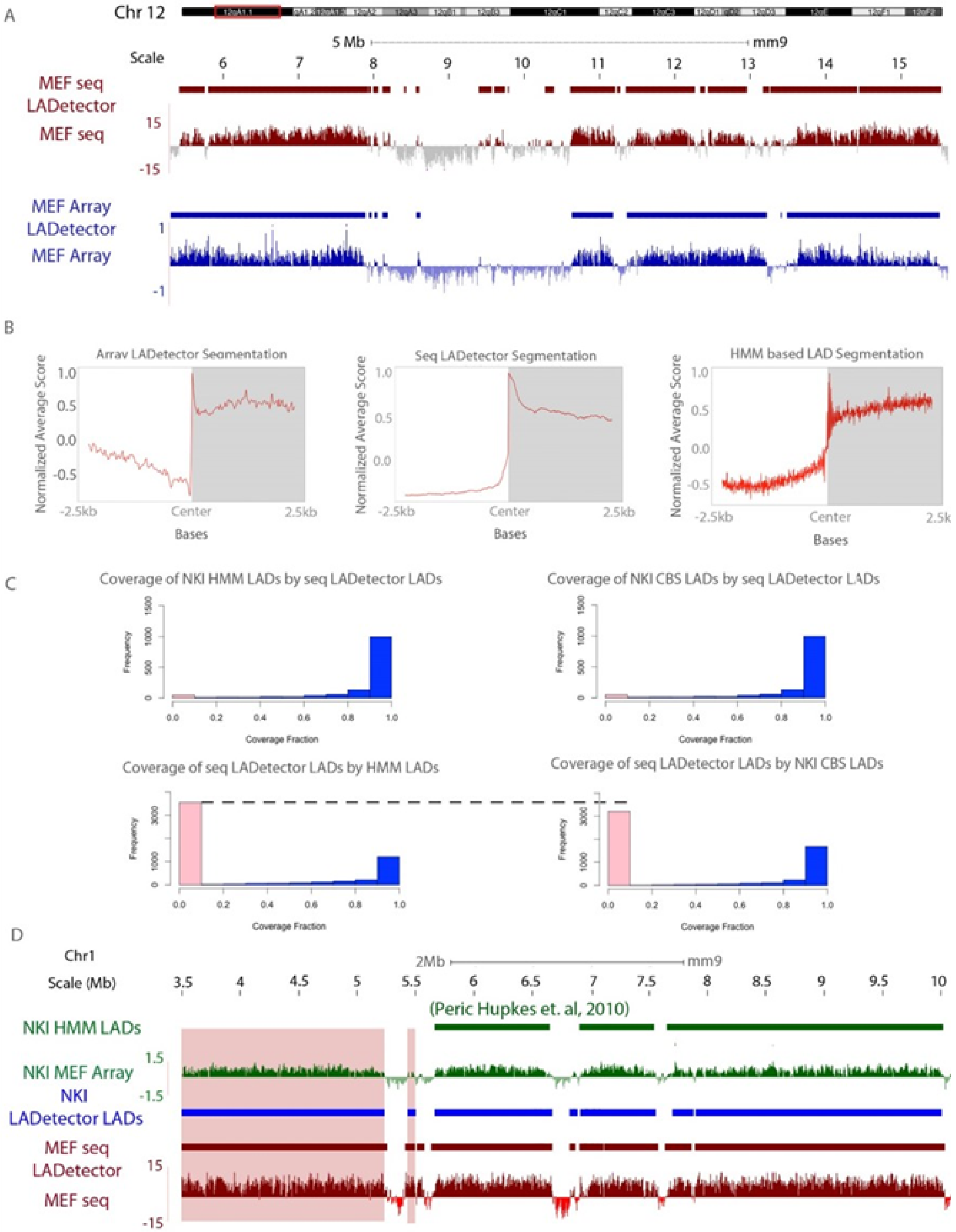
After hybridization to microarray, we also see that the *IgH* locus is enriched in LaminB1 signals (Figure 6c). Applying the LADetector we are able to define the *IgH* LAD locus on Chromosome12 from 114,461,016-117,403,240Mb. Evaluation of the pro-B cell type over the *IgH* locus by the LADetector yields no LAD regions. Over the entire microarray containing chromosomes 9-14, there are a total of 1,120 fibroblast LADs with a size range of 25 kilobasepairs (kbp) to 10 megabasepairs (mbp) (Figure 7)—25kbp was our cut-off to identify a region as a LAD. Data for Chromosomes 11 and 12 were published in (Harr et al. 2015)

Next, we confirmed that the LADetector could be used with the DamID-sequencing method devised and described by (XW reference) (Figure 8). Applying the LADetector to DamID-seq for mouse embryonic fibroblasts yields 5064 LADs over the whole genome. This number is likely higher in our data relative to other published studies because we are defining LADs as 25 kbp or larger, while a previous group sets this threshold at 100 kbp. Comparing our results to previously published HMM defined LAD regions (Peric-Hupkes et al. 2010), we note much overlap of Dam-LaminB1 signals with our results. However, we now provide data for regions not included in previously published data and with defined boundaries that visually align with the $\log_2$ ratio profiles. More than 90% of NKI MEF LADs (these are the custom array-based data from the van Steensel group using HMM algorithm to identify LADs) coincide with our MEF DamID-seq LADS with a coverage of 90-100% (Figure 8c, left panel). However, only 1763 out of 5064 of our DamID-seq LADs are covered by the NKI MEF data—indicating that we have identified additional regions missed by the algorithm, the design of the array or the 100 kbp cut-off set in that study. To determine where this discrepancy came from, we next used the LADs identified both data sets and plotted them against the signal intensities of the DamID LaminB1 interaction data (Figure 8b). Looking at a window of -2.5kb to +2.5kb spanning the LAD boundaries, the borders clearly separate LAD and nonLAD domains in a sharp, clearly delimited transition. Both the LADetector and the original HMM approach seems to accurately define LAD domains, but the HMM overlooks many of the LADetector domains. As mentioned, the original LAD data was based on custom arrays and so to determine if the LADetector has better sensitivity, we ran the previously published DamID log2 ratios through the LADetector. The resulting data more closely match our fibroblast data indicating that the LADetector is able to rescue some of these ‘lost’ LADs—and that only a portion of the missing data is due to our lower 25 kbp cut-off.

This initial analysis of LAD regions and establishment of the LADetector as a novel method for definition of binary LAD calls are foundational for work presented in this dissertation. MEF microarray data is used throughout this body of work along with other DamID data as specified throughout the text and additional observations of LADs and features are discussed in subsequent chapters.

Figure 8 LADetector Validation. Comparison between CBS and HMM based segmentation.

(A)Visual traces showing $\log_2$ *ratios of Dam-Lamin B1/Dam and identified LADs for a region in chr12 for MEF-array (blue) and MEF-sequencing (maroon) data. (B) Plots of the transition of average lamin B1 occupancy across all LAD borders (white: outside LADs, gray: inside LADs). (C) Histograms of LAD coverage (top: coverage of NKI MEF array – HMM based lads by Sequencing – CBS LADs (left) and vice versa (right), bottom: coverage of NKI MEF array-CBS lads by Sequencing-CBS LADs (left) and vice versa (right). Pink bars highlight LADs with zero coverage. (D) Traces of* $\log_2$ *score for LaminB1/Dam from NKI MEF array (green) and MEF-seq (maroon) with their respective LADs in the same colors above the traces of* $\log_2$ *score. Blue trace shows the LADs obtained in this region when the NKI MEF array data was input into the CBS algorithm.*



2.3 Methods

2.3.1 Preparation of DamID library

MEFs were purchased from ATCC (CRL-2752) and cultured according to their established protocols, in medium containing DMEM High, 10%FBS, Penicillin/Streptomycin and L-glutamate. DamID was performed using a modified version of the Nature Methods protocol (Vogel, Peric-Hupkes, and van Steensel 2007; Zullo et al. 2012; Harr et al. 2015). Specifically, we designed self-inactivating retroviral constructs pSMGV Dam-V5 (Dam-Only) and pSMGV Dam-V5-LaminB1 (Dam-LaminB1) to generate retrovirus using the Platinum-E packaging line (RV-101, Cellbiolabs). Supernatants containing viral particles were collected between 48-72 hours after transfection of the DamID constructs, and collection times were pooled. C57Bl/6 MEFs were incubated overnight with either Dam-only or Dam-LAMINB1 viral supernatant and 8μg polybrene. Cells were trypsinized from the plate and DNA was harvested using QIAamp DNA Mini kit (Qiagen 51304 and company), precipitated and resuspended to 1μg/μl using a nanodrop spectrophotometer to measure DNA concentration. 2.5ug of this genomic DNA was digested overnight with restriction enzyme DPN1 (R0176, NEB) and then heat-killed for 20 minutes at 80°C. Samples were cooled and then double stranded adapters of annealed oligonucleotides AdRt (5′-CTAATACGACTCACTATAGGGCAGCGTGGTCGCGGCCGAGGA-3′) (IDT) and AdRb (5′-TCCTCGGCCG-3′) (IDT) were ligated overnight with DPN1 digested fragments (T4 DNA Ligase 799009 Roche). After incubation the ligation was heat-killed at 65°C for 10 minutes, samples were cooled and then digested with DPNII for one hour at 37°C (R0543 NEB). This material was then amplified in ligation-mediated PCR using AdR_PCR oligo as primer (5′-GGTCGCGGCCGAGGATC-3′)

(IDT) and Advantage cDNA polymerase mix (catalog # 639105 Clontech). Amplicons were subjected to electrophoresis in 1% agarose gel/1XTAE to check size distribution of library and then column purified (QIAquick PCR Purification QIAGEN 28104). Once purified, material was checked for LAD enrichment using controls specific to either a LAD positive region (fiboroblasts and non-B cells) internal Immunoglobulin heavy chain *IgH* LAD region (*J558 1*, 5′-AGTGCAGGGCTCACAGAAAA-3′, and *J558 12*, 5′-CAGCTCCATCCCATGGTTAGA-3′) or a specific to a lamina-negative region in a LAD (also called Dip; *chr10:105245772_141bp_F*, 5′-AGGGACAGCCGTGGAGGAGC-3′, and *chr10:105245772_141bp_R*, 5′-CCGCACCGTCCGGTTCTCAG-3′) for validation prior to microarray hybridization and/or sequencing.

2.3.2 Hybridization to microarray

Dam-only and Dam-LAMINB1 samples were labeled with Cy3 and Cy5 using a random prime strategy, and DamID samples were hybridized to mouse whole genome tiling array 3 of 4 (mm8, part of chromosome 9 to part of chromosome 14; Economy Array; NimbleGen) using standard protocols. Arrays were scanned using a scanner (MS200_2), and probe intensity $\log_2$ ratios Dam-LAMINB1 to Dam only were obtained using DEVA 1.0.2 software (Roche NimbleGen). All experiments were performed two independent times.

2.3.3 DamID-seq

Library Preparation

Post-DamID amplified material was randomized by performing an end repair reaction followed by a ligation and sonication.-.5-5ug of column purified (QIAquick PCR Purification Kit: Qiagen, 28104) DamID material was end repaired using the NEBNext End Repair Module (NEB E6050S) following manufacturer's recommendations.-Subsequently, the end-repaired DNA was purified, again, using the QIAquick PCR Purification Kit (Qiagen, 28104).-1ug of the resulting DNA was then ligated in a volume of 20uL with 1ul of T4 DNA ligase (Roche, 10799009001) at 16'- The ligation mix was topped up to 200ul using ddH2O.-Sonication was carried out using the Bioruptor® UCD-200 at high power, 30s on, 30s off for 1 hour in a 1.5ml DNA lo-bind microfuge tube (Eppendorf).-The DNA was then transferred to 1.5 ml TPX tubes (Diagenode C30010010-1000) and sonicated for 4 rounds of 10 min long sonication with settings of high power, 30s on and 30s off.-The DNA was transferred to new TPX tubes after each round to prevent etching of the TPX plastic. The sonication procedure should yield DNA sizes ranging from 100-200 bp. After sonication, the DNA was precipitated by adding 20ul of 3M sodium acetate pH5.5, 500ul ethanol and supplemented with 3ul of glycogen (molecular biology grade, 20mg/ml stock) and kept at -80 o for at least 2 hours. The DNA mix is centrifuged at full speed for 10 min to pellet the sheared DNA with the carrier glycogen. The pellet was washed with 70% ethanol and then centrifuged again at full speed. The DNA pellet was then left to air dry. 20ul of 10mM Tris.Cl was used to resuspend the DNA pellet. 1ul aliquot of this resuspended DNA is diluted to be quantified using the Quant-iTTM PicoGreen ® kit. (Invitrogen, Molecular Probes, Cat No. P7589) Sequencing library preparation is performed using the NEBNext Ultra DNA library prep kit for Illumina (NEB, E7370S).

Mapping and Normalization

100 bp reads were mapped using an in-house written bioinformatics pipeline. First, each read was quality trimmed. This algorithm uses a sliding window of 3 nucleotides. The sliding window first advances from the 5' end of the read, removing the most 5' nucleotide until the mean of the scores of the nucleotides in a window is

greater than 30. The sliding window then advances from the 3' end and does the same operation. The quality trimmed reads were then filtered for reads greater than 25 nucleotides in length. The output of the trimming software is then fed into another program that detects and removes AdPCR primer sequences introduced during the DamID randomization procedure. This program looks for oligonucleotide sequences corresponding to any DamID primer or adapter sequences. Typically, any read that contains the adapter sequences dsAdR are concatemers of the adaptors and are filtered away. Any read that has an internal AdPCR primer sequence is split into different reads with the sequence prior to the primer as one read and the one after the primer as another. The output of this program is then used in a series of mapping and post processing steps. Mapping onto the mouse genome assembly, mm9, was done using Bowtie1 with default settings. Importantly, during the randomization procedure, we might end up with truncated AdPCR sequences at either 5' or 3' ends that cannot readily be detected from the previous filtering programs. This results in a small portion of our, otherwise, mappable reads unused in the first bowtie. The unmapped reads from the first bowtie are then processed by removing 13 nucleotides from the 5'end. These reads are then fed into Bowtie1 for the second time. Unmapped reads in the 2nd bowtie will then be used for 3' end processing and a final bowtie. However, we wish to recover the original sequence of the unmapped reads (ie non-5' trimmed sequences). Hence, the unmapped reads from the second bowtie were search for, in the unmapped reads of the first bowtie. Once these sequences have been retrieved, the 3' ends were trimmed by 13 nucleotides and passed through Bowtie1 for the last time. All 3 mapped sam files for each sample were concatenated and intersected using Bedtools with an interval file representing the mm9 genome that has been pre-binned by GATCs. The occurrences of the number of reads mapped to each bin is tabulated and normalized by the length of the bin and the number of reads for that sample. This score is then further normalized to the score of the respective bins obtained for the Dam only control to yield the relative occupancy of the protein of interest in each bin. A log2 ratio was obtained for each bin and stored in a bed file for display purposes and downstream bioinformatics analyses. Quality filtered reads (process of quality filtering described in the section Mapping of NGS reads) were converted to fasta format and input into the RepeatMasker program using the following command: RepeatMasker –species mouse input.fa

2.3.4 LADetector

DamID array signal intensity data were lifted over to mm9 using the Galaxy converter tool, and then, data from replicate arrays were averaged together (Giardine et al. 2005; Blankenberg et al. 2010; Goecks et al. 2010). DamID data were quantile normalized and smoothed using the preprocessCore R package (Bolstad 2003) and then segmented via a modified circular binary segmentation using the DNAcopy R package (Seshan and Olshen), which is an algorithm for identifying copy number difference, which "tests for change-points using a maximal *t*-statistic with a permutation reference distribution to obtain the corresponding *P*-value" (Venkatraman and Olshen 2007). A sliding window approach with a window size of 2 kb was used to combine neighboring segments, using in-house perl scripts. Code and accessory scripts provided in detail in Appendix A.2.

CHAPTER 3: LESSONS FROM B-CELLS. LAD DYNAMICS AND *DE-NOVO* LAD FORMATION

3.1 Introduction

Numerous studies have highlighted the importance of the nuclear periphery in developmental gene regulation (Reddy et al. 2008; Kosak et al. 2002; Szczerbal, Foster, and Bridger 2009; Williams et al. 2006; Meister et al. 2010; Zullo et al. 2012; Yao et al. 2011; Wang et al. 2011). Because all cells of an organism are derived from one totipotent progenitor (the fertilized egg), highly regulated transcription factor programs and epigenetic mechanisms are utilized to yield differential gene expression patterns allowing for diverse morphology and phenotype, i.e. differentiation (Figure 3). Dysregulation of these processes can lead to a wide range of developmental disorders. Protein composition of the nuclear lamina network, cell type specific transcription factors and a changing epigenetic landscape are all part of normal developmental gene regulation. The role that LADs play in this framework is just beginning to be understood and will be vital to our understanding of both development and disease processes.

Earlier cytological studies that focused on nuclear positioning and transcriptional output of tissue specific genes in various developmental systems strongly suggested that the nuclear periphery serves as a compartment for shunting and repressing developmentally regulated genes (Kosak et al. 2002; Szczerbal, Foster, and Bridger 2009; Williams et al. 2006; Meister et al. 2010; Yao et al. 2011). With the inception of the DamID technique, it not only became possible to generate comprehensive maps of molecular contacts between the nuclear periphery and the underlying genome, but also to identify differential LAD architecture between cell types (Reddy et al. 2008; Zullo et al. 2012; Peric-Hupkes et al. 2010). The subsequent profiling of LADs during differentiation of ES cells into astrocytes, for example, revealed the prevalence of a potentially core organizational architecture with discrete cell-type specific differences (Peric-Hupkes et al. 2010). Comparing these LAD maps throughout the neural development scheme, it was noticed that genes within domains that gain association with the nuclear lamina mostly become repressed, and genes within domains that lose peripheral contact become activated or poised for expression. This type of dynamic sub-nuclear localization of key developmental genes coupled with variable LAD maps throughout a developmental lineage provides evidence for a functional type of LAD, opposed to the original generally 'silent' definition of lamina associated domains. LADs have since been described to comprise of at least two different subclasses: 'constitutive LADs' and 'facultative LADs' (Meuleman et al. 2013). While much evidence exists for sub-classing of LADs, we feel these terms are a bit misleading given the paucity of cell types studied and the still ambiguous role of individual LADs and changing LAD landscapes. Between cell types, we find evidence of LAD regions that are common (cLADs) and those that are variable LADs (vLADs), which may play either structural and/or regulatory roles (Reddy et al. 2008; Harr et al. 2015; Zullo et al. 2012; Peric-Hupkes et al. 2010) (Figure 2). It will be important to analyze these vLADs to uncover mechanisms that allow for reorganization of these genic regions.

3.2 Variable LADs and B cell development

While there are many examples of changes in nuclear localization of developmentally regulated genes, protein composition at the nuclear lamina and chromosome structure, we choose to focus on pre-pro-B cells (EBF1-/-), pro-B (Rag2-/-), cells and mouse embryonic fibroblasts (MEFs). Our choice of B cell types and MEFs originates from our interest in studying nuclear architecture in the context of

B cell development. We know the immunoglobulin heavy chain locus is associated with the nuclear periphery in MEFs and is more centrally positioned during B cell development while the locus is actively recombined (Reddy et al. 2008; Harr et al. 2015). To further our understanding of overall nuclear architecture in development, I identified LADs in these cell types and compared their chromosome wide profiles for insight into organization changes that occur during development.

Using the DamID technique and analysis approach described in Chapter 2, we were able to compare LAD signatures across cell types and we noticed that there are a subset of LADs, the vLADs, that contain genes that are developmentally regulated, including our 'control locus' *IgH*. Of special note is that in EBF-/- cells, the *IgH* locus is in a LAD, indicating a level of organization not previously observed in the literature (Figure 9). Testing the localization of the LAD, we find that in many cases at least one allele associates with the nuclear periphery (Figure 9).

Intriguingly, initial examination of the genes contained within pro-B specific vLADs (relative to MEF LADs) yields Ikzf1 (Ikaros) and Bcl11a (B-cell lymphoma 11a), two key genes involved in B cell development. This observation prompted a further analysis of pro-B vLAD genes and a GO analysis provides a list heavy in factors that are important for regulating development, especially B cell, supporting our hypothesis that LADs are dynamic and serve as a regulatory compartment during developmental progression. In addition to vLADs, we also note there are common LADs (cLADs) that are LADed in multiple cell types, in this case both pro-B and MEFs. We hypothesized that cLADs and vLADs are distinct compartments, with different chromatin features/characteristics. As mentioned previously, other groups have since noted that LADs are able to be sub-divided into classes

Initial experiments aimed at mapping DamID profiles and comparing LAD maps across disparate cell types (B cells and MEFs) were completed by hybridization of material on microarrays, as described in Chapter 2. Data obtained in this way is limited by the genomic regions present on the array which in this case contains only chromosomes 9-14 and is repeat masked to not contain repeat elements and centromeres. While we know we have obtained quality data using microarray, our goal was to map genome-wide chromatin-NL molecular association maps. To do this, we employed a novel sequencing method developed in the lab. The results and regions in LADs largely agree between hybridization and sequencing, but with coverage over regions excluded from array.

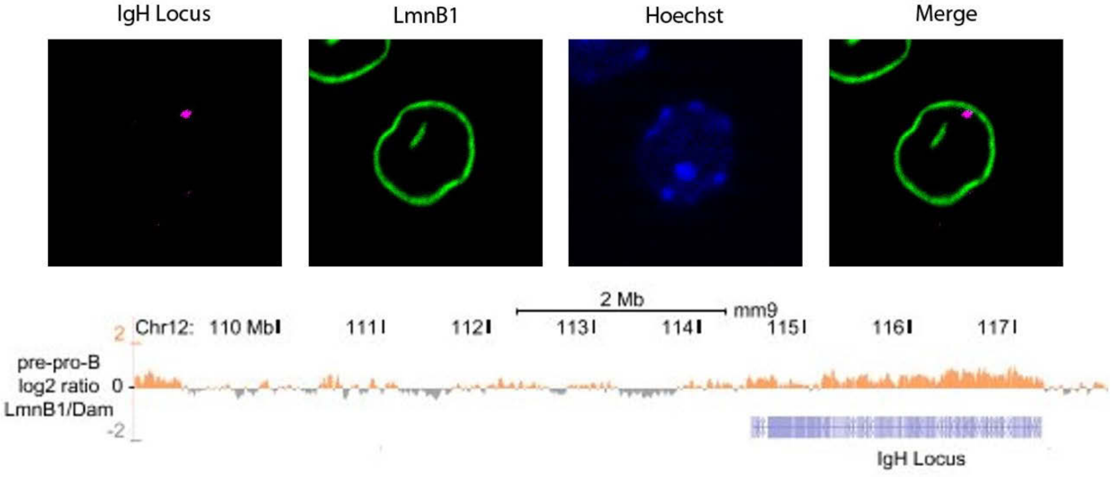


Figure 9 EBF Images

DamID data in pre-pro-B cell types depicts the IgH locus with positive associations with the nuclear periphery (bottom). FISH of the IgH locus(pink) in pre-pro-B cells shows cytological association with the nuclear periphery (LaminB1, green).

Using this new sequencing approach I chose to investigate the LAD profiles between pre-pro-B (EBF-/-) and pro-B cells (Rag2-/-). pre-pro-B and pro-B cells are at distinct but sequential stages of development within the B cell lineage, and are arrested at their specific stages by null mutations in either EBF1 or Rag2 that are crucial for developmental progression. The cells are easy to massively expand in tissue culture while maintaining genome integrity (measured by ploidy), and can be infected with DamID viruses and are therefore great candidates to explore genome rearrangements during development. By using these two cell types. By employing DamID-seq and the LADetector, I was able to identify 4180 new vLADs between pre-pro-B and pro-B cells, 2483 vLADs specific to pre-pro-B cells and 1697 specific to pro-B cells which may be important for B cell development (Figure 10, Appendix A.6). Included in this gene set is the *IgH* locus, which we have previously confirmed

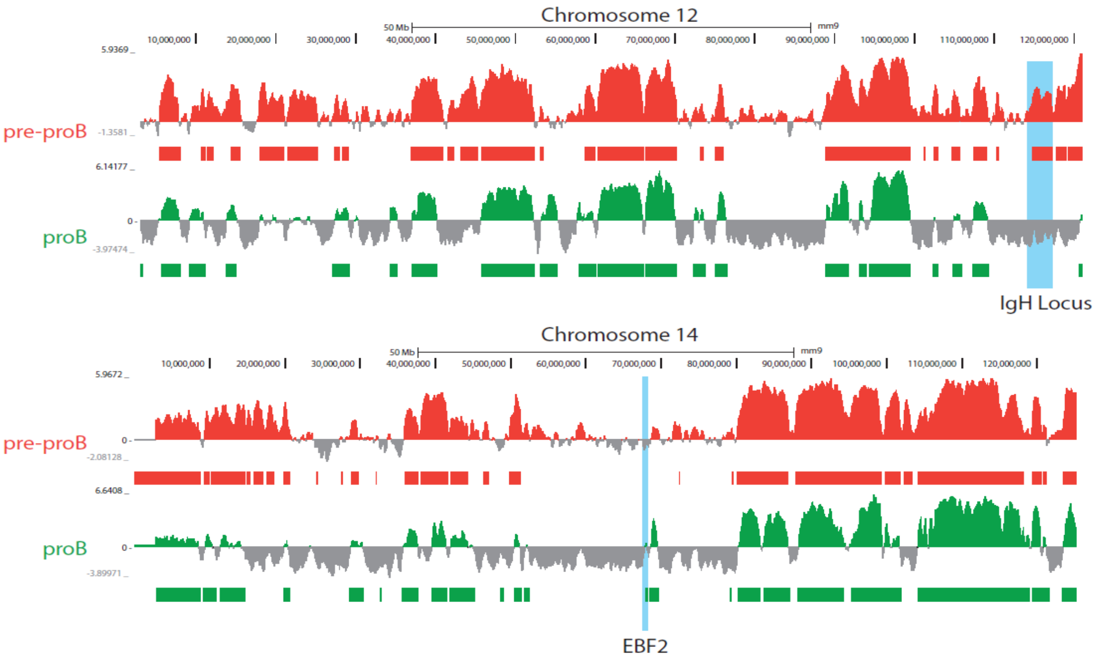


Figure 10 pre-pro-B and pro-B DamID profiles

DamID maps for pre-pro-B (orange) and pro-B (green) cells were generated and plotted across the genome. Regions highlighted in blue are vLAD regions with known importance for B cell developmental progression to be differentially LADed, as well as the EBF2 locus, a pre-pro-B specifically expressed gene which is in a LAD in pro-B cells (Figure 10 bottom).

3.3 Borders of LADs and *de-novo* LAD formation

3.3.1 Large, tandem, insertions of vLADs direct to the nuclear periphery

A close examination of the LAD and vLAD regions led to the observation that the vLAD regions are often on the edges of LAD domains. Because many of the

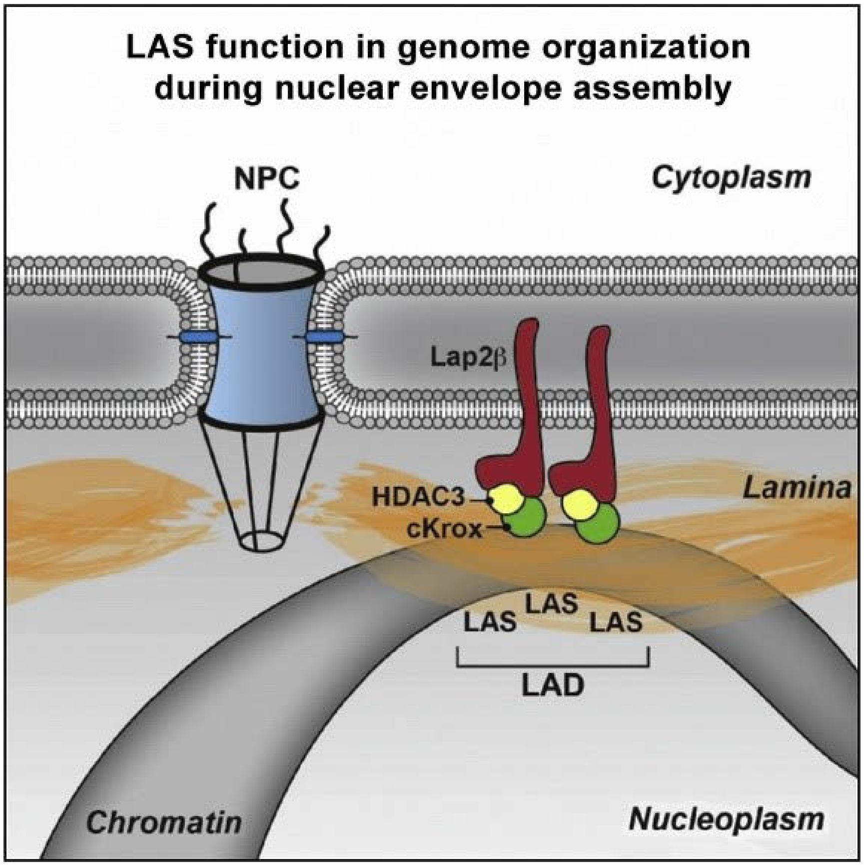


Figure 11 Lamin Associating Sequences direct to the nuclear periphery

Model depicting the interaction of multiple LASs in a LAD with the INM-lamina. GAGA motifs in LASs are recognized by cKrox, which interacts with HDAC3 and the INM protein Lap2β. HDAC3 is proposed to function both as an adaptor for lamina association as well as a transcriptional corepressor via its histone deacetylase activity.

developmentally regulated variable LADs (vLADs) between cell types occur on LAD edges, likely to enable shifting of these LAD border regions for accessibility to variable genes, we hypothesized that the study of border regions of vLADS would enable a greater understanding of how the dynamic genome is reorganized at the nuclear periphery (Peric-Hupkes et al. 2010). While evidence supports that gene activation and movement away from the peripheral zone are coupled, it is currently unclear whether activation precedes movement away from the repressive domain, and is a target of study (Kumaran and Spector 2008; Peric-Hupkes et al. 2010; Almouzni et al. 2013). No definitive 'LAD' zipcode has yet been identified across all LADs and it is important to note that, since cLADs and vLADs exhibit different responses to developmental cues, not all LADs are equal. It is therefore important to analyze vLADs specifically to uncover sequences and mechanisms that allow for reorganization of genic regions in a cell type specific manner. As an example, a recent study focused on the *IgH* and *Cyp3a* loci (which are both lamina-proximal in murine fibroblasts but nucleoplasmic in pro-B cells and hepatocytes, respectively) uncovered dispersed Lamina Associated Sequences, LASes that can direct repositioning of ectopic regions to the nuclear periphery when randomly integrated into the genome (Zullo et al. 2012). The LAS sequences identified were enriched in GA di-nucleotides, which is striking given that LAD domains are relatively A/T rich. It is tempting to speculate that such LAS sequences may be important for establishing peripheral compartmentalization of genomic regions during cellular differentiation. It is, however, still unclear how decisions pertaining to cell type specific LADs are being made given an (almost) identical genome across cell types of an organism. This study showed it was necessary to uncover more such LAS elements from vLADs and to determine whether such sequences are truly sufficient and what proteins mediate reorganization into a *de novo* LAD. The above mentioned study also uncovered roles for a cell type specific transcription factor (Zbtb7b or cKrox), a histone deacetylase (HDAC3) and an INM protein (LAP2β) in mediating *de novo* interactions with the nuclear lamina (Figure 11).

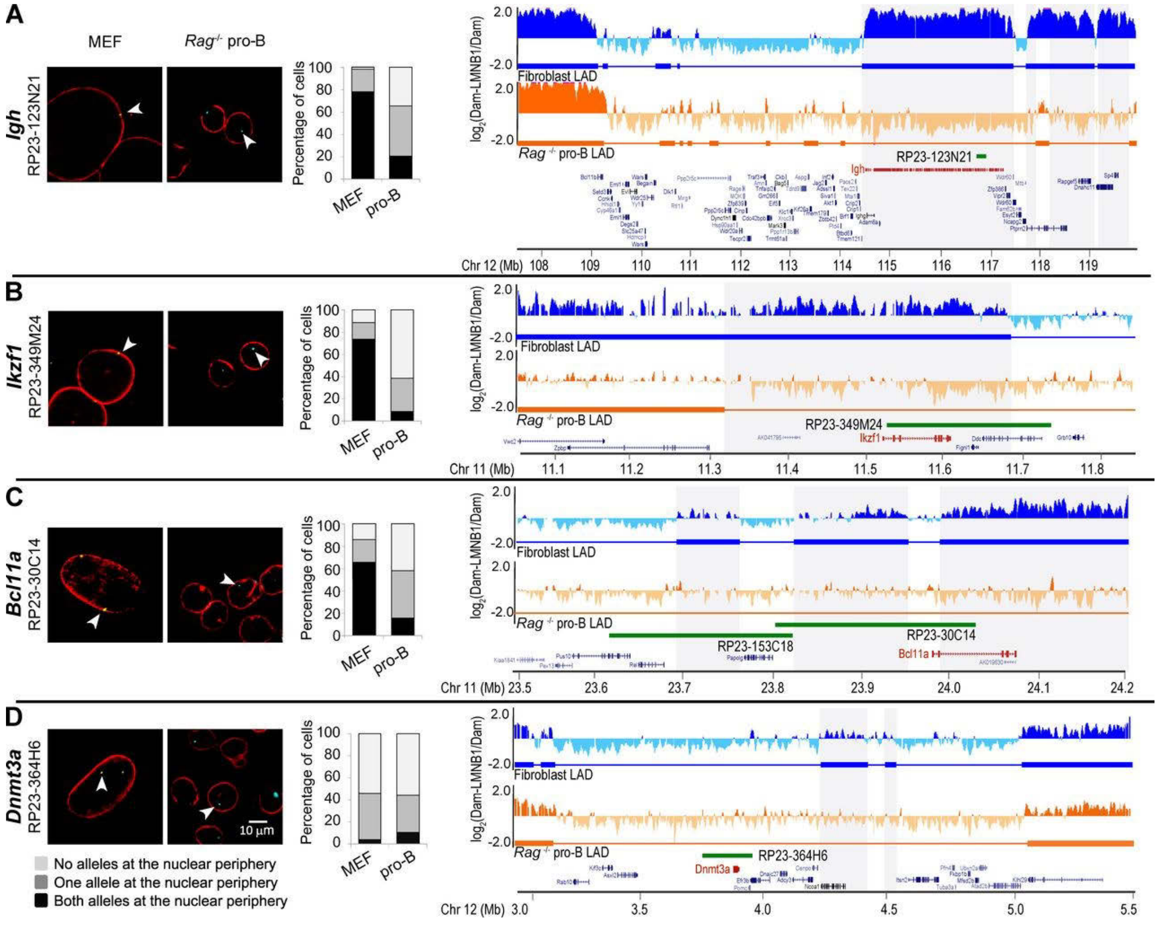
3.3.2 Single insertions of vLAD sequences can direct to the nuclear periphery

A closer study of vLAD regions between pro-B cells and MEFs was initiated to elucidate factors and genic elements involved in positioning of chromatin to the nuclear periphery in mammalian cells, with a particular focus on dynamically reorganized border regions of LADs. This work identifies genomic regions containing developmentally regulated genes that reside in regions that are dynamically lamina associated depending on cellular state (vLADs) and, therefore, have regulated nuclear positioning. In particular, by studying vLADs covering the IgH, Ikaros (Ikzf1) and B cell CLL/lymphoma 11A (Bcl11a) loci, which are positioned at the border of fibroblast-specific vLADs and are no longer associated with the lamina in pro-B cells (Figure 12 A).

These regions are ideal candidates for interrogating sequence-dependent mechanisms of positioning to the nuclear lamina. We also identified a region spanning the *Dnmt3a* gene, which is not in a LAD, but inactive (by array and quantitative PCR [qPCR] analyses), in our cell lines (Figure 12 D). 3D immuno-FISH analyses confirmed that the disposition of these endogenous genomic regions

Figure 12 Both Fibroblast and pro–B cell genomes contain vLADs

(A–D) Shown are regions containing the Igh, Ikzf1, *and* Bcl11a *loci from fibroblast-specific vLADs. (left) Representative images of 3D DNA immuno-FISH of endogenous in fibroblast and pro–B cells. FISH probes detecting the indicated regions are depicted (arrowheads), and the nuclear lamina is demarcated by LAMINB1 (red). Quantitation of peripheral association was determined by overlap of FISH probe and LAMINB1 (*n ≥ *50). (right) DamID detection of LADs* *log*$_2$*(Dam-LAMINB1/Dam) mean ratios from three experiments for fibroblasts (blue) and pro–B cells (orange). Traces above the 0 line indicate a region in a LAD. Solid blue and orange bars underscore LADs in fobroblasts and pro–B cells, respectively. Genes are indicated as transcripts (blue), and our gene of interest is red. BAC locations are indicated by green bars, and gray shading indicates an fobroblast-specific vLAD. Chr, chromosome.*

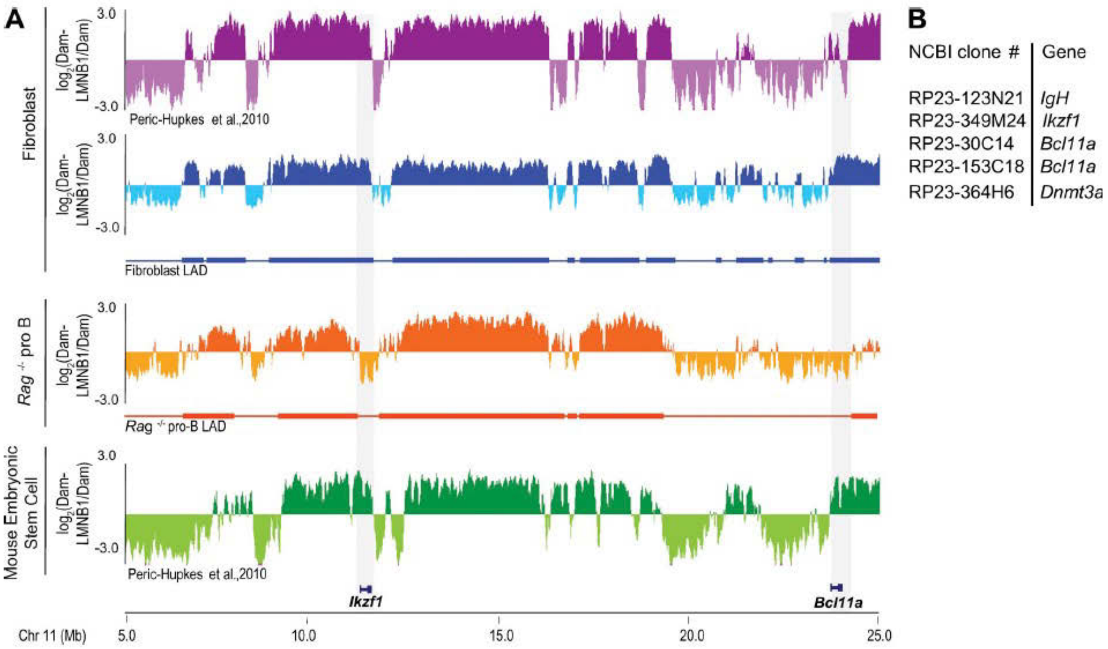


in MEFs and pro–B cells are as predicted from the molecular DamID contact maps (Figure 12). It is important to note that the loci/regions we have identified in MEFs as lamina proximal by DamID are at the nuclear periphery in a majority of fibroblasts (65–80% have both alleles at the lamina), whereas these same regions display negative lamina association by DamID and an association rate of 30% in pro–B cells, reflecting the background level of "association" with the lamina by cytological measures. Both of these cell types are primary cells and may display different levels of association with the lamina when compared with data published from subcloned cancer-derived cell lines (Kind et al. 2013). Finally, gene expression microarray data from pro–B cells and fibroblasts demonstrate differential expression levels for Bcl11a, Ikzf1, and IgH, in agreement with previous studies and consistent with the nuclear lamina facilitating or reflecting a transcriptionally repressed state (Medina and Singh 2005; Johnson et al. 2004; Johnson et al. 2008; Reynaud et al. 2008; Heydarian et al. 2014).

Interestingly, we have noted that many vLADs are at LAD borders, suggesting that these regions may be especially important in dynamic genome reorganization (Peric-Hupkes et al. 2010). The *IgH* locus is unusual in that the locus itself comprises the LAD (3 Mb) and the entire LAD reorganizes in pro–B cells, whereas *Ikzf1* and *Bcl11a* are more typical examples of vLADs, with only a portion of the LAD (proximal to the border) being lost in the permissive pro–B cell type (Figure 12).

DNA sequences from vLAD borders target to the nuclear periphery

To elucidate the ability of specific LASs to direct targeting of sequences to the nuclear periphery, we integrated bacterial artificial chromosome (BAC) DNA constructs carrying sequences from fibroblast-specific vLAD border regions covering the *Ikzf1* (RP23-349M24) and *Bcl11a* (RP23-30C14 and RP23-153C18) loci into the genome of NIH3T3-derived C57BL/6 fibroblasts (ATCC CRL-2752; Figs. 13 B and 14, A and B).



NCBI clone #	Gene
RP23-123N21	*IgH*
RP23-349M24	*Ikzf1*
RP23-30C14	*Bcl11a*
RP23-153C18	*Bcl11a*
RP23-364H6	*Dnmt3a*

Figure 13 DamID profiles of Fibroblasts and pro-B cells

Lamin-associated domains, as determined by DamID compared in three cell types. (A) a 20-kb window shows that fibroblast DamID traces (blue) align with previously published data from this region (purple; Peric-Hupkes et al., 2010). DamID data are represented by log₂ (DamID-LaminB1/Dam) mean ratios from three experiments, shown for fibroblast (blue) and pro-B cells (orange). Traces aboved the 0 line indicate a region in a LAD. Mouse Rag2-/- pro-B cells (orange) and mouse ESCs (green; Peric-Hupkes et al 2010) highlight the presence of Ikzf1 and Bcl11a in fibroblast-specific vLADs (vLADs shaded). Solid blue and orange bars are LADetector LADs. Genes are indicated as transcripts below the traces. (B) BACs to the LAD border regions used in 3D DNA immuno-FISH and nuclear repositioning assays.

Figure 14 BACs covering developmentally regulated vLAD borders target to the nuclear periphery

*(A) Representative images of random cointegration of BACs and lacO arrays. Arrowheads indicate the lacO array location as detected by EGFP-LacI binding. LAMINB1 (red) marks the periphery of the nucleus. The inset is a 300× magnification of the EGFP-LacI focus. (B) Quantitation of peripheral association was determined by overlap of EGFP-LacI focus and anti-LAMINB1 signal ($n \geq 50$; *, $P \leq 0.001$). The dotted line indicates the frequency that a nontargeting sequence associates with the nuclear periphery (lacO arrays). Error bars indicate SD of two experiments by two individuals. (C) DNA fragments covering the border region of the fobroblast-specificBcl11a vLAD contain LAD-ed and non–LAD-ed regions. Most of these fragments do not cover the Bcl11a gene. Histogram traces are $\log_2$ (Dam-LAMINB1/Dam), and a consecutive positive signal indicates a LAD region in the fibroblast. Solid blue bars represent binary LAD calls. The Bcl11a locus (dark blue) is shown above the LAD call, and the position of the RP23-153C18 and RP23-30C14 BACs used to generate the smaller fragments are shown in green. Smaller DNA fragments tested for re-positioning are shown in pink (generated from the RP23-153C18 BAC) and orange (generated from the RP23-30C14 BAC). Chr, chromosome. (D) Quantitation of random integration of the indicated DNA fragments (orange) from BAC RP23-30C14 in C57BL/6 fibroblasts ($n \geq 50$; *, $P \leq 0.001$). Error bars are the SD of imaging data as scored by two individuals. The dotted line is the approximate peripheral association of lacO alone when randomly integrated into fibroblast cells. (E) Quantitation of IF data from TCIS clones Y and 12 after switching the indicated DNA fragments (pink) contained within BAC RP23-153C18. TCIS-NS are the TCIS clones Y and 12 containing the nonrecombined or nonswitched (NS) TCIS system. Error bars indicate SD. The dotted line is the ap-proximate peripheral association of a nonrecombined TCIS insert. *, $P \leq 0.001$.*

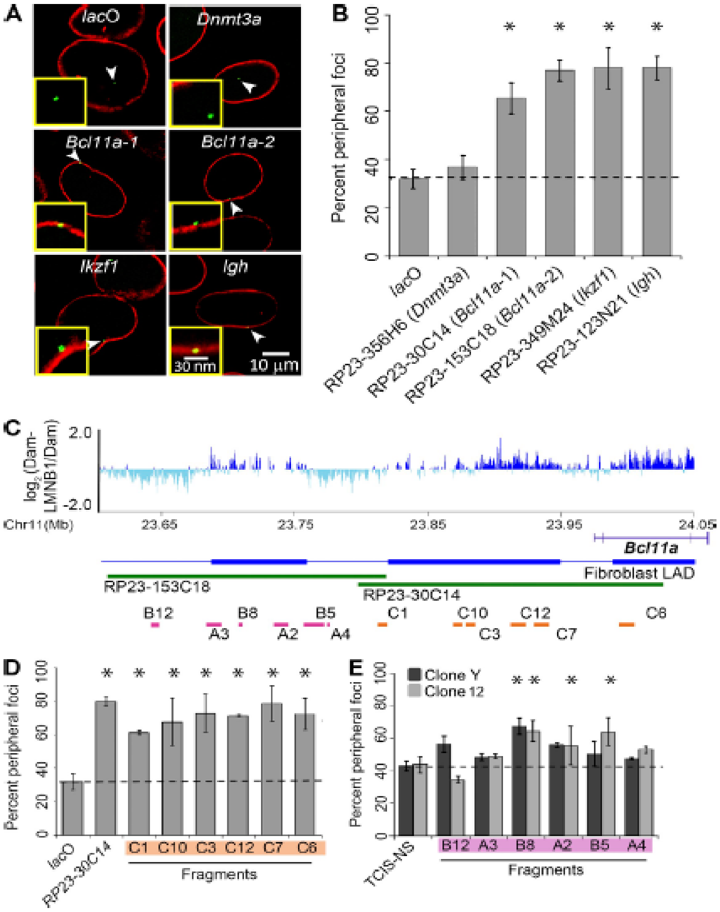
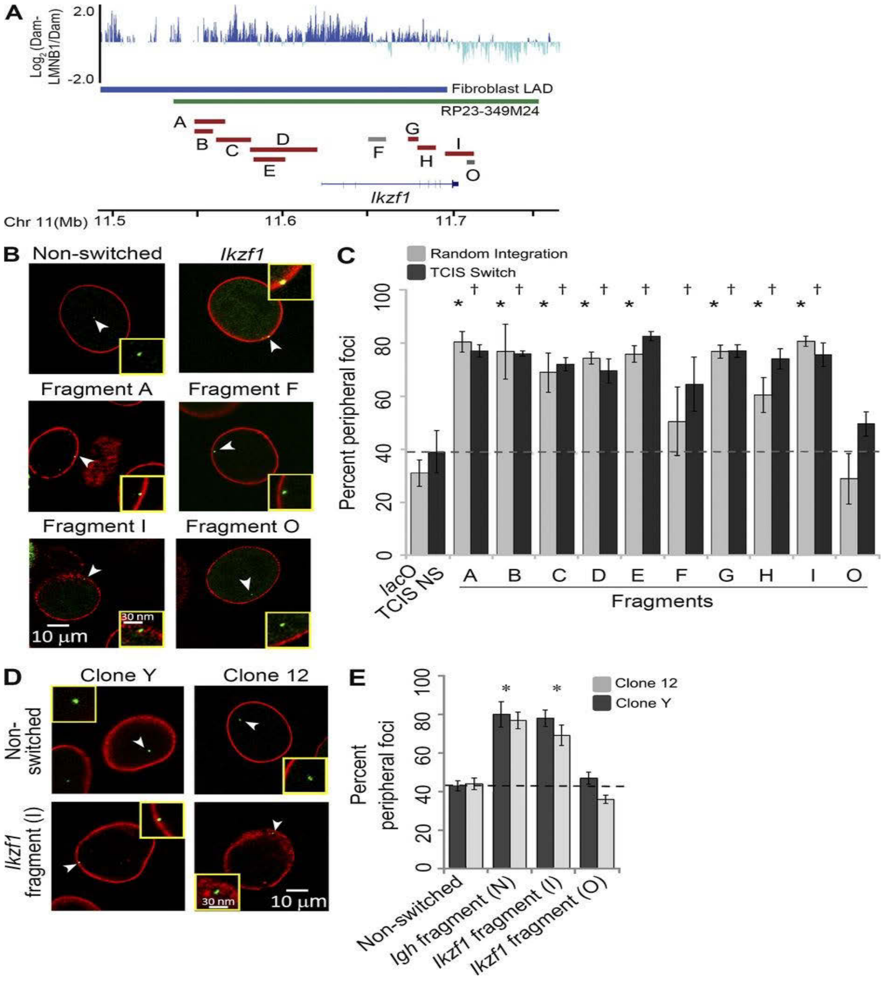


Figure 15 Ikzf1 LASs target to the nuclear periphery in fibroblasts

(A) Ikzf1 (A–I and O) fragments span the border region of the fibroblast-specific Ikzf1 vLAD. Histograms are $\log_2$ *(Dam-LAMINB1/Dam), and the blue bar underscores the LAD. The Ikzf1 locus (blue) and overlapping BAC used to generate the smaller fragments are shown (green). Ikzf1 LASs are red, and nonassociating fragments are gray. (B) Representative images showing the disposition of lacO arrays (arrowheads, green) and LAMINB1 (red) in the original TCIS clone as well as nuclei harboring randomly integrated Ikzf1 BAC fragments (top) or TCIS clones with site-specific recombination of Ikzf1 (A, F, I, and O). The inset shows 300× magnification. (C) Quantitation of peripheral association was determined by overlap of EGFP-LacI foci and LAMINB1 (*$n \geq 50$*). Fragments were tested for their ability to target to the nuclear periphery by random integration or by directed integration (TCIS). Error bars indicate SD.* $P \leq 0.001$ *(asterisks show random integration, and crosses are TCIS switch). NS, nonswitched. (D) Representative images of IF for the disposition of Ikzf1 (I) or Igh (N) LAS recombined into the TCIS sites in clones Y and 12. Arrowheads show EGFP-LacI binding lacO arrays (green) at the TCIS site and LAMINB1 (red). Insets are 300× magnifications. (E) Quantitation of peripheral association of Ikzf1 (I) or Igh (N) LAS in clones Y and 12 (*$n \geq 50$, $P \leq 0.05$*). Dotted lines are approximate peripheral association of the nonrecombined TCIS insert.*



As controls, a BAC from the distal, but internal, portion of the *IgH* locus (lamina-associated positive control, RP23-123N21) and another covering the *Dnmt3a* locus (non–lamina-associated negative control, RP23-364H6) were also used (Figure 12 and 13)(Zullo et al. 2012). These BACs were randomly cointegrated into fibroblasts cells with hygromycin-selectable *lacO* arrays, as previously described (Zullo et al. 2012). The *lacO* arrays serve as docking sites for EGFP-LacI, thus enabling quick identification by microscopy of the disposition of the integrations. An overlap of LaminB1 signal and an EGFP-LacI/*lacO* focus was scored as peripheral (Figure 16a and b). *lacO* arrays integrated alone served as a control for expected distribution of random integrations, and these were found at the periphery with a frequency of ~30% (Figure 14b). Importantly, an integrated BAC covering the *Dnmt3a* locus is centrally disposed despite its inactive status, reminiscent of the disposition of the endogenous locus (Figure 14b and Figure 12d). We note that a previous study (Zullo et al. 2012) showed that the genomic region around the neuronal PAS domain 3 gene (*NPAS3*) was not in a LAD in fibroblasts (though inactive) and was unable to reposition an ectopic site in this cell type, in agreement with our results for the genomic region around *Dnmt3a*. Moreover, *NPAS3* is in a LAD in pro–B cells (GEO accession no. GSE56990). These data suggest that, perhaps, sequences from domains that are not in a fibroblast LAD are unable to confer lamina-proximal association in fibroblasts, regardless of transcription status or LAD status in alternate cell types. In contrast, BACs covering vLADs have a 60% (*Bcl11a*-1) to 80% (*Ikzf1*, *Bcl11a*-2, and *IgH*) propensity to be lamina proximal, mimicking the disposition of endogenous loci (Figure 12 and 14b). Given that these BAC LASs are able to mediate association of ectopic sites to the nuclear lamina, we next asked whether we could elucidate smaller sequences capable of such targeting. Both the *Ikzf1*- and *Bcl11a*-containing BACs demonstrating potential to direct to the nuclear periphery were further fragmented (*Ikzf1 (A–O)*;Figures 15a and 14c), and these smaller potential *Ikzf1* LASs were randomly cointegrated with the aforementioned *lacO* arrays. The *Ikzf1* fragments tested ranged from 900 bp to 30 kbp and were derived from regions interior to the vLAD border as well as those crossing and outside of the border regions (Figure 15, A–C, *Ikzf1 (I)* and *(O)*). Interestingly, the fragments seem to show repositioning potential that correlated with the LAD status of the endogenous region (Figure 15b and c, gray bars). Noteworthy is the non-relocating *Ikzf1 (F)* whose sequence falls in a break, or dip, in lamina association in an otherwise contiguous LAD region (Figure 15 b and c, gray bars). Sequence from *Ikzf1 (O)* falls outside of a LAD, and it does not relocate to the periphery (Figure 15a-c, gray bars). We therefore hypothesize that *Ikzf1 (O)* lacks sequences sufficient to target (address) to the nuclear periphery, whereas the *Ikzf1 (I)* LAS retains this information. Similar results were obtained for the BAC containing sequences from the LAD border covering the *Bcl11a* locus (Figure 14d).

One caveat to the above mentioned experiment, and previously published experiments, is that the LASs tested have all been randomly integrated and likely represent many copies of the sequence at any given insertion site (Figure 11, Zullo et al. 2012; Bian et al. 2013). Therefore, it is difficult to determine whether an identified LAS was truly sufficient for targeting to the periphery or whether multiple copies of the LAS conferred a novel DNA or chromatin state that was itself a signal for compartmentalization. Intriguingly, many LADs contain duplicated genes or loci, for example, the *IgH* and *Cyp3a* loci, and are enriched in long interspersed nuclear elements, suggesting that multimeric sequences may be a signal for directing to the lamina (Zullo et al. 2012). However, there are regions of the genome that do not appear to be highly duplicated that are in a LAD (e.g., *Ikzf1* and *Bcl11a* LAD regions), and we therefore hypothesize that a single LAS may contain sufficient information to direct lamina-proximal targeting.

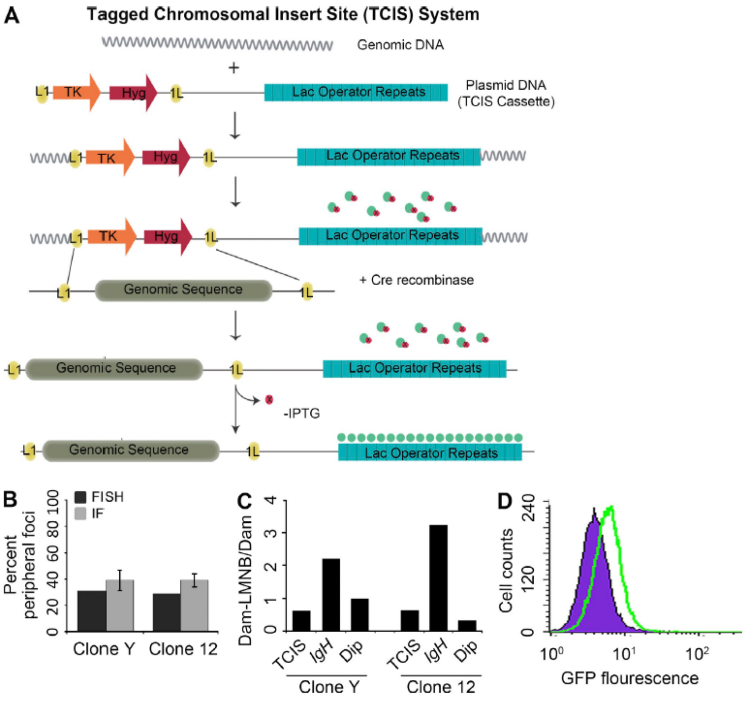
LAS from vLAD borders are sufficient to target to the periphery

To enable an experimental test of this hypothesis, a novel technique was developed called, TCIS, in which we can integrate a single DNA fragment of choice into the genome by directed recombination. Fibroblast clone Y and 12 were identified as carrying a single integration site by qPCR and microscopy (immunofluorescence [IF] or live cell imaging of GFP-enriched foci. These parental clones display the "default" disposition of the single integrated TCIS system, which is away from the nuclear lamina (Figure 12b and 29b and c). We note that only a subset of the cells display EGFP-LacI foci detectable by 3D microscopy, as previously described (Belmont et al., 1999). Therefore, to ensure that we are able to measure disposition accurately using IF and EGFP-LacI foci as a readout, we demonstrated that 3D immuno-FISH to the *lacO* sequences reflected the same disposition as our IF strategy (Figure 16b). Although we do not know the integration sites, the empty TCIS is not associated with the nuclear lamina by DamID analyses, thus the default association is away from the nuclear lamina (Figure 16c). Using this system, we are able to "switch" DNA segments into the TCIS system with high efficiency in as little as 5 days, with selection (Figure 16c). Thus, the TCIS system enables testing of a single noniterated LAS for its ability to target an ectopic genomic site to the nuclear periphery. Moreover, each LAS tested will be in the exact same genic location, thus mitigating misinterpretation of results based upon possible position effects caused by differential integration sites.

The previously described *Ikzf1 (A–O)* fragments were therefore integrated into TCIS clone Y expressing EGFP-LacI to enable detection of disposition of the *lacO* sites (Figure 15, A–C, black bars). These potential LASs in single copy showed relatively the same probability of targeting to the nuclear periphery in fibroblast cells as they did in multiple copy random integrations (Figure 15C). The *Ikzf1 (I)* LAS (border) and a control from *IgH* LASs were tested in both of our clones Y and 12 (Figure 15D and E; Zullo et al., 2012); additionally, fragments from broader border regions near *Bcl11a* were integrated into clones 12 and Y, and similar results were obtained (Figure 11E). The transitional *Ikzf1 (I)* LAS, which covers the outermost edge of the *Ikzf1* LAD border region, was then further dissected to identify specific DNA elements with roles in establishing and/or defining a LAD. Specifically, 2.5-kbp subfragments covering the entire *Ikzf1 (I)* were switched into clone Y. The smaller *Ikzf1 (I)* LAS fragments comprised of sequences derived from regions adjacent to borders, but outside of LADs, are unable to mediate repositioning (Figure 17B). We note that *Ikzf1 (I)* LAS fragments 3 and 4 straddle the defined border region. These results indicate that there is both a sharp edge delimiting lamin-associated regions and that sufficient information required for repositioning to the nuclear periphery resides at or inside LAD boundaries in small LASs (<2.5 kbp).

Figure 16 The TCIS system allows for the site-specific recombination of a DNA sequence of interest.

(A) The TCIS system is composed of two previously de-scribed technologies: the lacO/LacI system (lac operator/Lac repressor) and recombination-mediated cassette exchange. This system allows us to tag a chromosomal region with lacO segments, recruit LacI fusion proteins, and to site-specifically integrate specific single-copy DNA sequences of interest by Cre-mediated recombination into inverted loxP sites. (Robinett et al., 1996; Feng et al., 1999). Specifically, we integrated a linearized construct containing 256 lacO repeats contiguous with two inverted loxP sites interrupted by thymidine kinase (TK) and hygromycin (Hyg) genes for negative and positive selection, respectively. TCIS cell lines were generated by introducing this linearized construct into NIH3T3-derived fibroblast cells followed by positive selection with hygromycin. Individual isolated clones were screened by qPCR for copy number, and single sites of integration were verified by fluorescence microscopy of EGFP-LacI, which binds to and accumulates on the integrated lacO array, thus marking the insertion site. (B) Quantitation of IF versus FISH shows comparable positional determination of the TCIS system location (n ≥ 50). Error bars indicate SD. (C) TCIS insertion sites are centrally disposed and not in a LAD, as determined by DamID. qPCR to a region of the TCIS locus is not enriched in regions of the genome marked by Dam-LAMINB1 when compared with Dam treatment alone. Primers to the Igh locus, a lamina-associated region in fibroblast cells, are used as a positive control. Primers to non–lamina-associated regions (dip) are used as a negative control. The data shown are from a single representative experiment, out of three. (D) Efficient and successful switching is tested by recombining in a GFP coding gene into the TCIS region. To determine the efficiency by which we can introduce new DNA sequences, we cloned a cyto-megalovirus-EGFP expression cassette into a vector containing inverted loxP sites that corresponded to the loxP sites in the TCIS integration (switch vector), and fibroblast cells were cotransfected with this construct along with a vector encoding Cre-recombinase into TCIS clone Y or clone 12. Efficient switching takes place within 5 d and is guaranteed by negative selection with 1 μM ganciclovir for 24 h (Feng et al., 1999). Flow cytometry shows a shift in GFP fluorecence in the whole population (green) compared with nonswitched TCIS clones (purple). The data shown are form a single representative experiment out of three.



Cell type–specific transcription factors and proteins involved in nuclear architecture and scaffolding are involved in sequence targeting

Figure 17 Positioning by small LAS fragments at the edge of a LAD border and how potential protein candidates were identified for further functional analyses.

(A) The lamina-targeting Ikzf1 fragment I was further segmented (fragments 1–9) and switched into TCIS clone Y. (B) Quantitation of peripheral association was determined by overlap of EGFP-LacI focus and anti-LaminB1 signal ($n \geq 50$). NS is nonswitched; I and O are the larger fragments ($n \geq 50$). Error bars are the SD of imaging data as scored by two individuals (, $P \leq 0.001$). (C) MotifSuite analysis of LAS reveals binding motifs for YY1, BTB/POZ binding domain proteins, and CTCF. The occurrence and distribution of the identified motifs (horizontal ticks) are indicated along the fragments. (D) Fold enrichment of identified motifs in fragments (A–O and I) relative to random regions of chromosome 11 away from LAD borders from either MEME-generated motifs or from the transcription factor binding motif databases Factorbook and JASPAR. For comparison, motifs on known YY1 responsive elements sur-rounding the Surf1/2 gene and the Emu enhancer from the IgH locus size matched to fragment I, are shown. Dotted red lines are a fold enrichment of 1. (E) DamID determined traces in fibroblast (blue) and Rag2-/-pro–B cells (orange). fobroblast and pro–B LADs are indicated by solid blue and orange bars, respectively. Ikzf1 locus (blue) is below the LADs. Peripherally targeting fragments (A–I, red) from the vLAD containing Ikzf1 and nontargeting fragment O are in gray. CTCF ChIP-Seq data are shown in green (data show peaks at the border of the fibroblast-specific vLAD in MEFs and Rag2-/- pro–B cells; Robertson et al., 2007 [GEO accession no. GSE31039] and Lin et al., 2012 [GEO accession no. GSM987805]).***Figure on next page.***

We next aimed to determine enrichment of protein binding motifs within

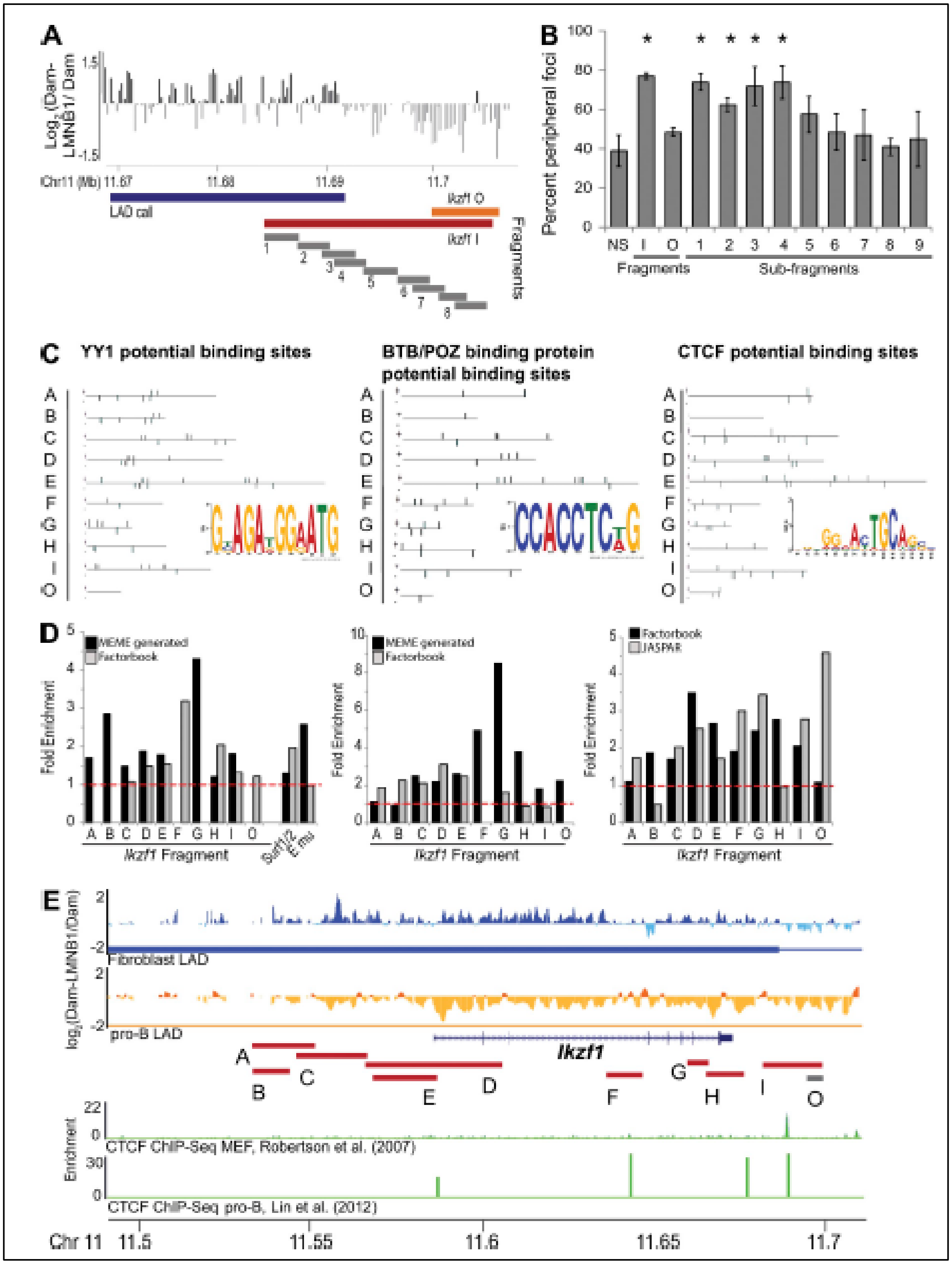
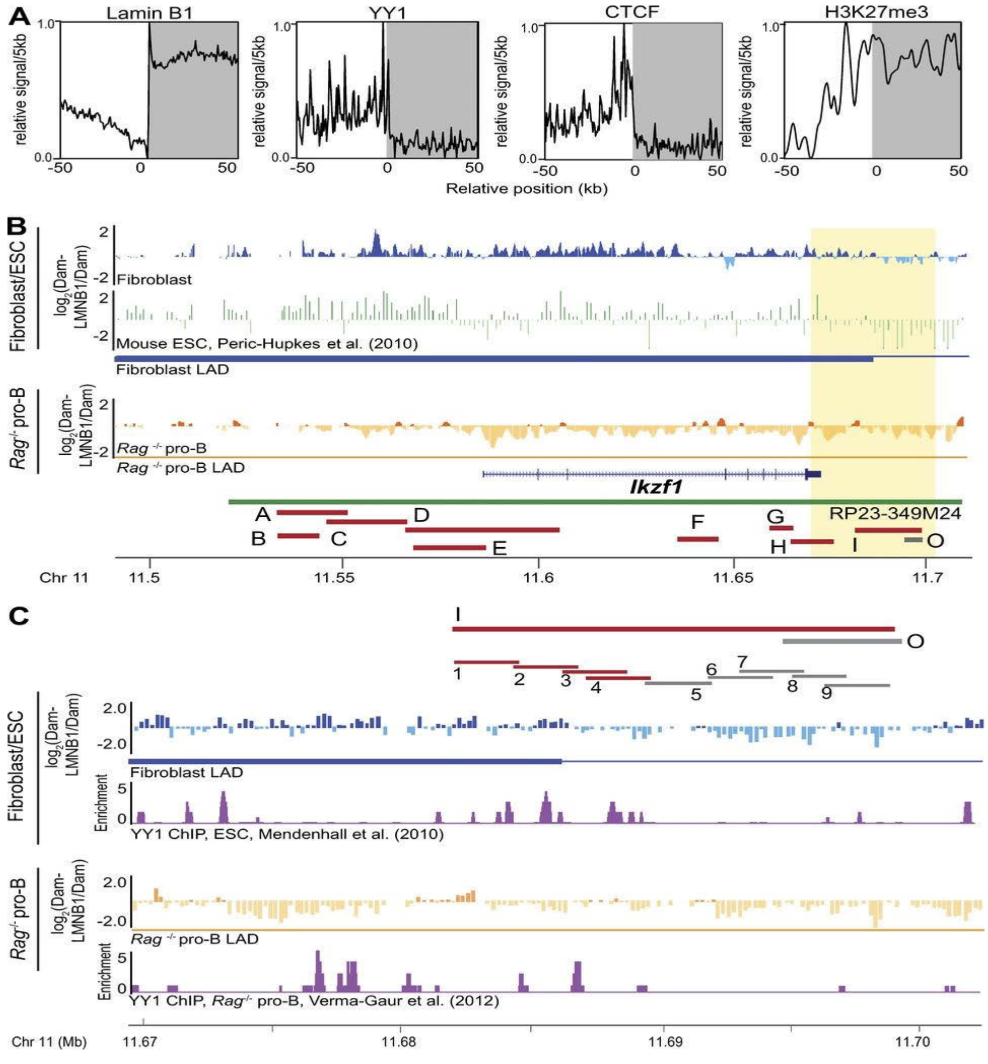


Figure 18 YY1 binding sites are enriched in LAS.

(A) Profiles of aligned LAD border regions (chromosomes [Chr] 9–14; left and mirrored right border regions combined) are shown for LAMINB1 binding, YY1, and CTCF binding site density and H3K27me3. To align LAD borders, genome-wide positions of all analyzed features were converted to coordinates relative to the nearest border. Gray area and positive coordinates, inside LADs; white area and negative coordinates, outside LADs. (B) DamID histograms in fibroblast (blue), ESC cells (green; GEO accession no. GSE17051; Peric-Hupkes et al., 2010), and pro–B cells (orange). Histograms are log$_2$ *(Dam-LAMINB1/Dam), and a positive signal indicates a LAD region. The solid blue and orange bars underscore LADs. The Ikzf1 locus (blue) and BAC used to generate the smaller fragments (green) are shown below the fragments. LASs are depicted in red, and nonrepositioning fragments are depicted in gray. (C) Depicts magnification of the Ikzf1 LAD border (light yellow from B). Subfragments (1–9) of the Ikzf1 (I) LAS are shown relative to ChIP-Seq data from ESC, and pro–B cells show YY1 binding site enrichment (YY1, GEO no. GSM628031; pro–B, GEO no. GSM1002560; Mendenhall et al., 2010; Verma-Gaur et al., 2012).*



Ikzf1 (A–E and *G–I)* LAS that would serve to identify potential protein candidates for further functional analyses. An initial search using MEME and TomTom

identified YY1 (Ying-Yang 1), CTCF, and cKrox/ThPOk/Zbtb7b (as well as other BTB/POZ domain proteins) binding site motifs as among those enriched in these sequences (see Materials and methods; Figure 17 C and D). Not surprisingly, we also identified several binding sites for specific B cell development proteins (not depicted). Both CTCF and Zbtb7b binding site motifs were previously identified in LADs/LAS (Guelen et al. 2008; Zullo et al. 2012). Intriguingly, YY1 is known to have roles in genome regulation in many cell types, including both gene activation and repression, and has been implicated to recruit polycomb repressive complex 2 (PRC2) to chromatin to promote H3K27me3 modification (Satijn et al. 2001; M. L. Atchison 2014; M. L. Atchison 2014; L. Atchison et al. 2003; Srinivasan, Pan, and Atchison 2005; O'Meara and Simon 2012). Next, we sought to identify all potential YY1 binding sites in LAD border regions via pair-weighted matrix motif analyses. Specifically, we analyzed the disposition of predicted YY1 and CTCF binding sites (Figure 14 C and D) over chromosomes 11 and 12 using MEME Suite and Genometricorr (Claeys et al. 2012; Favorov et al. 2012). Using the MEME-identified motifs, we generated maps of sites along each fragment using the MAST algorithm (Figure 17C). In addition, because the output of MEME simply indicates a statistically significant enrichment of a given motif, we next analyzed the fold enrichment of identified motifs in our fragments relative to random regions of chromosome 11 away from LAD borders from either MEME-generated motifs or from the transcription factor binding motif databases Factorbook and JASPAR (Figure 17D; Sandelin et al., 2004; Wang et al., 2012; Mathelier et al., 2014). For comparison, we show enrichment of these MEME and Factorbook motifs on known YY1 responsive elements surrounding the *Surf1/2* gene (*Surfeit locus protein 1 and 2*) and the Emu enhancer from the *IgH* locus size matched to fragment I, for comparison (Figure 17D; Cole and Gaston, 1997). Using MotifSuite, we estimate an approximately twofold enrichment of YY1 binding sites at LAD borders (±10 kb) relative to chromosomal background (unpublished data; Claeys et al., 2012). Finally, the statistical correlation package Genometricorr indicates that YY1 binding sites, either derived from our MEME analyses or from the Factorbook database of binding motifs, are more enriched relative to LAD borders compared with what would be expected by random chance ($P < 0.001$; Favorov et al., 2012).

These initial lead candidate analyses led us to next identify actual YY1 occupancy relative to LADs. Leveraging publicly available data of YY1 binding and LaminB1-DamID (e.g., LAD) maps in embryonic stem cells (ESCs) along with our data and publicly available data in pro–B cells, we found that high peaks of YY1 binding often correlated with LAD boundaries (Figure 18A) (Mendenhall et al. 2010; Peric-Hupkes et al. 2010; Vella et al. 2012). We note that in the *Ikzf1*, *Bcl11a*, and *IgH* loci, the LAD configuration in ESCs mimics those seen in fibroblasts (Figure 18B, top). In addition, we note that the smaller relocating fragments (fragments 1–4), some of which, by bioinformatics analyses, were not identified as enriched in YY1 binding sites, nonetheless display YY1 occupancy in both non–B cell types, in this case ESCs, and pro–B cells (Figure 18C). It is thus very important to note the obvious: there are a large number of regions actually occupied by YY1 both inside and, more predominantly, outside of LAD border regions and, in the case of previously published results in ESC cells, YY1 occupancy is often associated with active promoter regions (Figure 18A; Vella et al., 2012). Interestingly, although *Ikzf1* is in a LAD in ESCs, it is not in pro–B cells, yet in both cell types, these regions have demonstrated YY1 binding (Figure 18C). This likely reflects both the diversity of

YY1 functions and its potential dual roles in regulating these regions. We also note, as has been previously reported, that we find CTCF binding motifs to be enriched at LAD borders (Figure 18A and 17C and D; Guelen et al., 2008). In all cases, the putative and determined binding sites were shown to be enriched in LAD border regions; however, it is quite evident that these regions are far from the only regions bound by these factors. Given these and previous data, we suspected that targeting to the lamina may depend upon on a combination of cell type–specific factors (such as BTB-POZ domain proteins; Figure 17C and D) as well as epigenome/genome organizers, such as YY1, PRC2 components (e.g., EZH2), lamins, and/or CTCF (Figure 17E). However, it was also clear from these analyses that simply trying to determine bioinformatically (motif or occupancy analyses) the roles of these proteins in LAD establishment would be problematic.

Further in-depth studies of YY1 in the lab shows that YY1 is enriched in these regions and direct recruitment of YY1 to a single site (YY1-eGFP-LacI) is able to reposition to the nuclear periphery. Specifically, YY1 knockdown experiments ablate ability to reposition. Additionally, knockdown of Lamin A/C, and not Lamin A (construct generated by Dr. Xianrong Wong from the Reddy Lab) and treatment with DZNep (Ezh2 inhibitor) or Bix-01294 (G9a inhibitor) also are able to inhibit peripheral repositioning. Taken together these experiments identify a mechanism involving YY1, H3K27me3 and H3K9me2/3in establishment and maintenance of LADs (Figure 19).

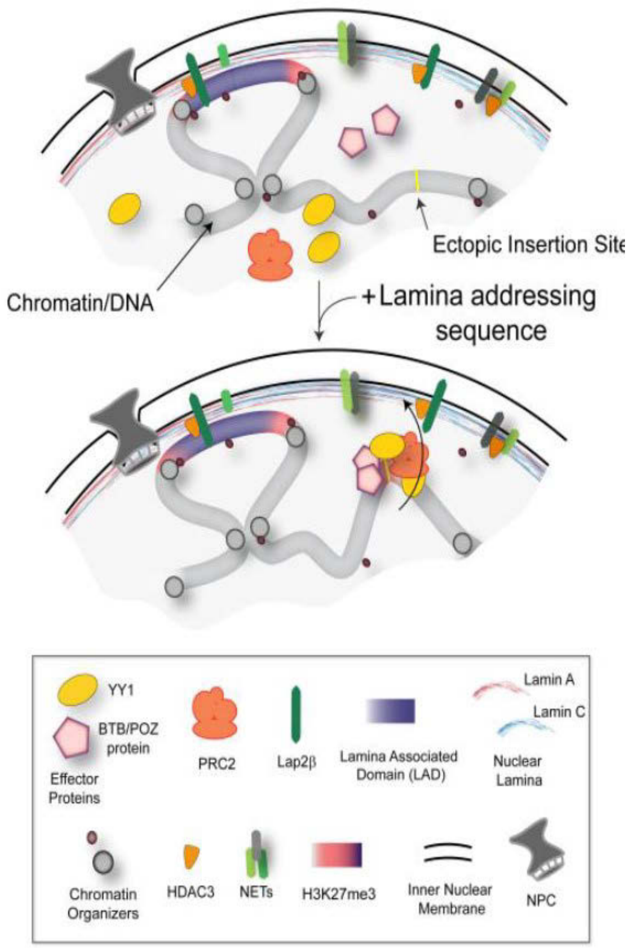


Figure 19 A speculative model for directed reorganization of chromatin by YY1.

A cross section of a portion of the interior of a fibroblast cell shows chromatin as a lamina associated domain (LAD, dark blue) or a non-lamina associated region (gray). Chromatin organizing factor, CTCF, and epigenetic regulators, Ying-Yang 1 (YY1) and Polycomb Repressor Complex (PRC2) are ubiquitously expressed. Cell type specific BTB/POZ type factors are present in the specified cell state (fibroblast, top). An ectopic insertion of a Lamina associated DNA fragment into an ectopic site (yellow), leads to accumulation of cell-type specific factors, such as BTB-POZ domain proteins of Zbtb7b, at the fragment containing their respective enriched binding sites. These cell type specific transcription factors may aid in YY1 recruitment or stabilization at these regions. YY1 would then recruit PRC2 enabling subsequent H3K27 tri-methylation and lamina association (bottom). There is also a requirement for H3K9me2/3 and the interaction of these two facultative heterochromatin marks (bi-valency) may be important for LAD formation and/or maintenance. Intriguingly, we also uncovered a potential role for LMNC (or LMNA/C levels) in this process.

3.4 Methods

DamID, LAD definition and FISH were performed as described in previous chapters.

3.4.1 Analysis of LADs and genomic features

YY1, CTCF, and H3K27me3 ChIP data were tested for statistically significant overlap of LADs in fibroblasts using the GenometriCorr package (Mendenhall et al., 2010; Peric-Hupkes et al., 2010; Favorov et al., 2012; Vella et al., 2012; Simon et al., 2013). The GenometriCorr package applies multiple spatial tests of independence including an absolute distance test (i.e., if two elements such as LADs and YY1 sites are a fixed distance from each other), projection test (i.e., testing for significant overlap between these two positions assuming they represent single points points), and the Jaccard test (testing for correlation of these two positions assuming that they are not points but instead occupy some interval of the genome). In addition to these statistical tests, the intensities of the DamID and ChIP peak data were plotted against bioinformatically determined LAD border regions (±50,000 kbp) to generate intensity profiles of the tested binding data for CTCF, YY1, H3K27me3, and LAMINB1 using the Genomation R package (Akalin et al. 2015). 200 bins were generated over the entire border interval (±50,000 kbp), and signal intensities of binding data within each bin were averaged and plotted.

3.4.2 Motif identification

BAC-derived fragments DNA tested for repositioning effects were analyzed for known and de novo motifs, performed with MEME Suite and MotifSuite (Timothy L. Bailey et al. 2009; Claeys et al. 2012). Specifically, sequences from relocating fragments were analyzed using both MEME Suite (MEME [Multiple EM for Motif Elicitation]) using default parameters. Identified motifs were compared with the expected frequency in chromosome 11 background (because the tested fragments were from this chromosome), generated using the MotifSuite background generator tool CreateBackgroundModel. Enrichment of the targeting versus background and nonrelocating fragments was determined by using a 0.5 threshold parameter. Only motifs that displayed a twofold enrichment were considered for further evaluation. The identified motifs were then mapped to the fragments with the MAST program (Motif Alignment and Search Tool) in the MEME suite (Bailey and Gribskov 1998). We then further confirmed the enrichment using randomly identified sequences in chromosome 11 away from LAD border regions and subjecting these to the same motif mapping via MAST. Only motifs identified as enriched over background on relocating fragments were further examined to identify proteins that may bind to these identified motifs using TomTom motif comparison software (Bailey et al., 2009).

3.5 Discussion

By identifying variable LADs across multiple cell types we have been able to begin to understand the dynamics of nuclear reorganization during development. Single genes and loci important for cell identity and lineage commitment have been studied and described to have differential positioning based on cell state. Developmental programs such as myogenesis, neurogenesis and immune development employ the use of the nuclear periphery for key genes, but previous studies have only identified these regions using cytological and low throughput techniques. By employing DamID through B cell development and in non-related cell types, we are able to study study peripheral localization of chromatin genomewide and on a molecular level to give us new and insightful information about genome organization. We have been able to identify novel, differentially positioning large regions of chromatin, and also confirmed that some of these regions do in fact contain genes that are important to be highly regulated. A very interesting result when comparing LADs gained and lost is that many of the differential regions occur on the edges or borders of LADs. Through parsing single DNA sequences from these vLAD borders we have been able to identify sequences for their ability to target and scaffold chromatin to the nuclear periphery, and termed LASes (Lamin Associating Sequences). We have shown that these regions rely on protein complexes in a complicated mechanism for direction to the periphery. A combination of histone modifications (H3K27me3 and H3K9me2/3), and cell-type specific adaptor proteins, such as Zbtb7b and YY1, come together on LAS sequences form a *de novo* lad.

Zbtb7b (also known as ThPok) encodes a BTB-POZ domain protein that can act as a transcriptional repressor or activator and recognizes $GA_{(n)}$ sequences (Matharu et al. 2010; Melnick et al. 2002). The transcriptional repressor mGCL (murine Germ-Cell-Less), another BTB-POZ domain protein, also interacts with Lap2ß and Emerin in the INM, prompting the intriguing possibility that this large family of differentially and developmentally expressed proteins may play a role in LAD architecture and function (Kimura et al. 2003). In addition, the BTB-POZ domain has been shown to recruit PRC2 (Polycomb Repressive Complex - responsible for H3K27me3) to chromatin, leading to the compelling possibility that targeting of LASes by these proteins leads to H3K27me3as well as association with the peripheral zone (Boulay et al. 2012). Interestingly, in *Drosophila* neurons, the neural competence factor hunchback (*Hb*) becomes repressed and lamina-proximal concordant with down-regulation of Distal Antenna (Dan) (Kohwi et al. 2013). Dan contains a ‘pipsqueak’ GAGA DNA binding motif that competes with BTB-POZ domain proteins for its target sites, and enforced expression of Dan prevents the lamina-proximal positioning and repression of *Hb* (Lehmann et al. 1998). LAS-containing regions, therefore, likely recruit specific factors (e. g. Zbtb7b or Dan) that in turn either promote (Zbtb7b) or inhibit (Dan) association with the peripheral zone (Figure 2). In addition, these cell type specific transcription factors could recruit chromatin remodelers for the induction of large scale chromatin changes concurrent with either localization to or away from the peripheral zone. Moreover, epigenetic state may be the overriding factor in the ‘decision’ to be relegated to the peripheral zone, and LAS sequences with specific protein partners may merely act as a molecular switch for inducing chromatin signatures that drive chromatin to the peripheral zone. In either case, it appears that some sort of combinatorial information (protein binding or epigenetic state, for instance) on top of the LAS sequences is needed to discriminate between domains that remain nucleoplasmic and those that are destined to become LADs in a cell type specific manner. It is likely that more cell type specific factors (both the previously mentioned NETs and transcriptional regulators) will be identified in regulating the dynamic LAD landscape, both in development and disease.

CHAPTER 4: FUNCTIONAL CHROMOSOME ORGANIZATION IN SINGLE CELLS

4.1 Introduction

The above DamID data experiments result in molecular contact maps of regions of chromatin with the INM in a population of cells. Important to note, these data capture all interactions from the time the construct was introduced, until cells are harvested and DNA is extracted for downstream analyses. What is unknown is if the regions determined to be in molecular contact with the lamina reflect a chromosome organization that is present in each cell, if the average genome conformation over the population where individual cells show a more divergent organization, or if transient interactions comprised a significant amount of our positive signal. Typically, verification of higher-order organization from genome wide data such as LAD data has been through traditional DNA-immuno-FISH, using Bacterial Artificial Chromosomes (BACs) as probes to detect a specific region, LAD or non-LAD, and measuring its coincidence with nuclear structure such as the periphery (Reddy and Feinberg 2013). This approach can confirm the associations of that specific region, but genome-wide data has yet to be mapped back and visualized in a single cell. Additionally, no one has shown functional conformation of a chromosome in a single cell, specifically whether LAD and nonLAD regions occupy different sub-domains as would be predicted if the bioinformatics data represents what occurs in single cells.

Very recently, efforts have also focused on the organization of chromatin into self-interacting domains or modules using Hi-C or other chromosome conformation capture (3C) based techniques (van Berkum et al. 2010). Unlike canonical ChIP assays or DamID, which rely on knowledge of a protein and/or modification of interest to target in the assay, Hi-C maps genome-wide DNA-DNA interactions, irrespective of the proteins or scaffold mediating these interactions. The resulting 'interactome' generated by such a study yields a large dataset of chromosomal interacting regions. One level of organization uncovered by such studies are TADs (topologically associating domains) which are on the order of 100kb to several megabases in size (Dixon et al. 2012; Sexton et al. 2012; Nora et al. 2012). Intriguingly, decades ago similar sized domain organization was detected by painstaking FISH analyses and it is tempting to speculate that these topological domains correspond to those same large chromosome loops(Cremer and Cremer 2010). By deconvolving Hi-C derived genome-wide association maps, several attempts have been made to predict a general structure of chromosome domains and folding in the nuclear volume. What is universally missing from these experiments is the ability to identify functional chromosome organization. One study has attempted to model chromosome structure based on the Hi-C-derived domain mapping and overlapping existing chromatin data (ChIP and lamina associations) which suggests preferred positions of chromosomal subdomains (Hu et al. 2013). However, chromosome conformation *in-situ* is still a mystery and proof of any functional organization has remained elusive. Here we report on a novel approach to detecting chromosome conformation *in-situ* using tiled oligos based on bioinformatic data obtained from DamID. The resulting chromosome paints in single cells reveal a functional organization of the chromosome territory only hinted at by population based assays such as Hi-C, ChIP and DamID. In addition, these chromosome paints can be used to identify disruptions in this architecture and reveal information on topological domain structure.

4.2 Population Wide Genomics in the Single Cell

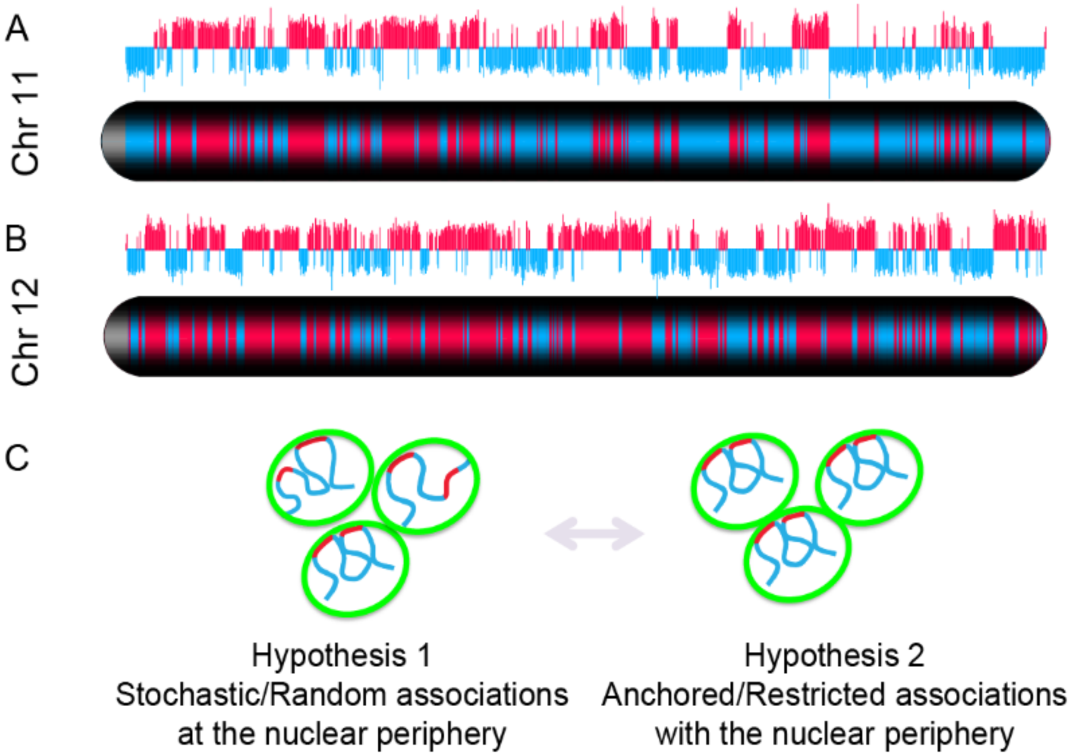


Figure 20 LAD Organization Hypothesis Testing

Molecular contact map Log$_2$ ratio plots for chromosomes 11 and 12 determined by DamID (panels A and B, top) were analyzed to define LADs. LADs are depicted in chromosome ideograms to show potential banding patterns (panels A and B, bottom). Organization of the LAD domains is unknown and banding patterns do not suggest segregation of LAD (red) and nonLAD (cyan) domains, therefore we can accept two separate hypothesis for 3D organization of interphase chromosomes: Hypothesis 1, the population of the cells demonstrate stochastic associations at the nuclear periphery where there is no one uniform organization and log$_2$ ratio plots indicate the average signals, or Hypothesis 2, LADs have anchored or restricted associations with the nuclear periphery, where most cells in the population exhibit similar organization (Panel C).

As mentioned above, taking structural-based genome-wide bioinformatic data that has been mapped back to the genome in 2D has given some insight to genome architecture, but we still do not know if the bioinformatics data reflects true 3D structure and conformation. While relational data can be obtained from HiC (inter-intra-chromosomal interactions) and DamID (chromatin-lamina interactions), these methods are based on populations of cells and require substantial assumptions on organization to model a 'preferred' chromosome conformation. In fact, a previous study has utilized both of these types of data to create a spatial model of how a chromosome may look in a cell and indeed, cross-comparing Hi-C and LAD data has yielded one of the most robust models of chromosome conformation (Hu et al. 2013). What is missing from even the best model is how well the 'preferred' conformation of the population is reflected at the single cell level. To enable such an experimental test, we utilized our lamina-chromatin maps in murine fibroblast cells (Figure 20a, Figure 20b, and Figure 22). These maps largely agree with those previously published but include more regions by virtue of the density of the microarray used, and our analysis provides a more precise determination of start and stop locations of LAD domains by using the LADetector (Figure 11) (Peric-Hupkes et al. 2010; Harr et al. 2015). We decided to use the LAD regions defined by the LADetector to design oligonucleotide library based FISH probes for both LAD and nonLAD regions (Figure 21a and b). We chose this approach after attempting to directly use DamID material as probe unsuccessfully, which has also been previously documented (Figure 21c) (Guelen et al. 2008). Put simply, LAD and nonLAD regions were bioinformatically defined using DamID hybridized microarray data. The DamID libraries were generated from mouse embryonic fibroblast populations. Based on genomic intervals of LADs and nonLADs, repetitive elements and other sequences

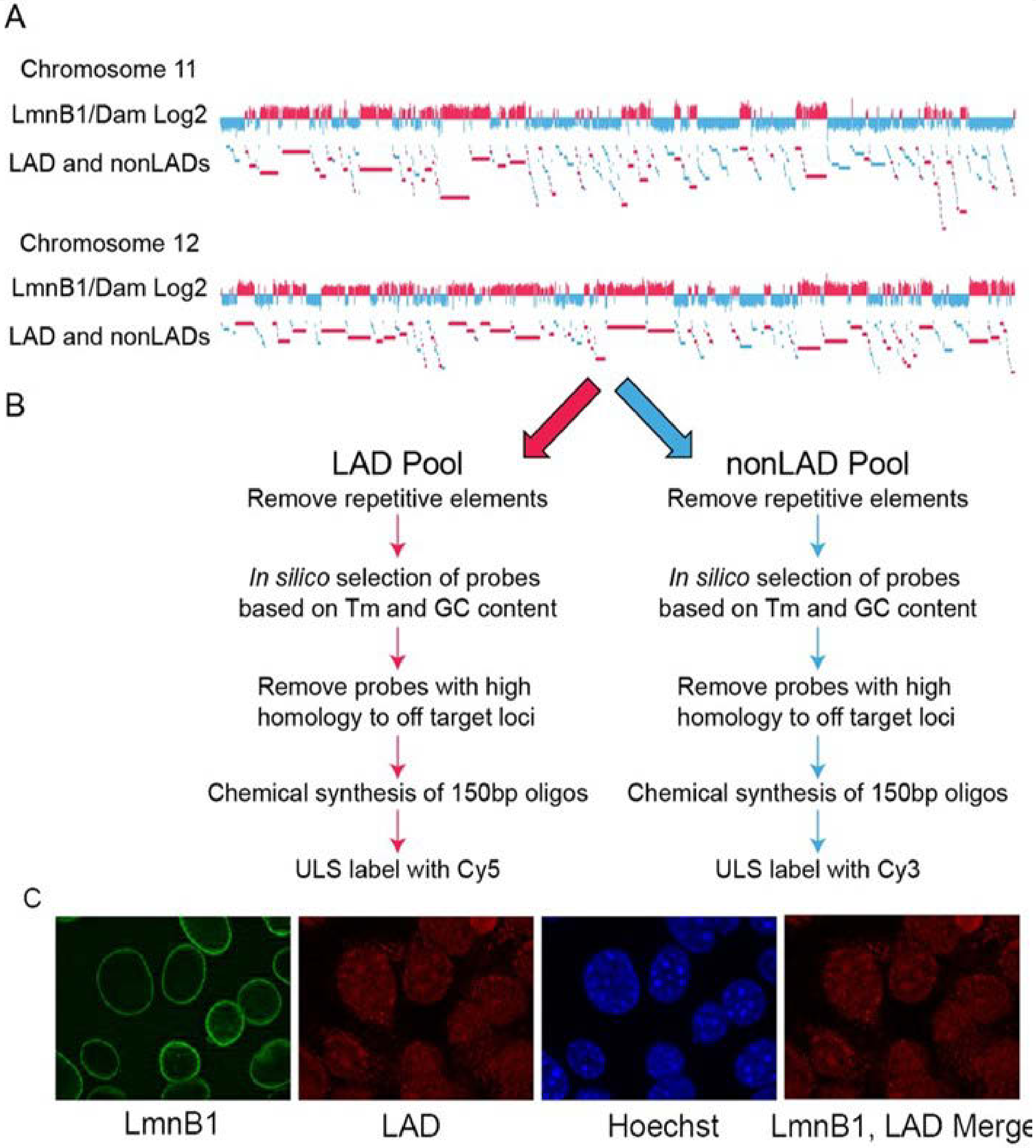


Figure 21 Probe Design

LAD (red) and nonLAD (cyan) regions were defined across chromosomes 11 and 12 (panel A) and divided into two separate tracks. Both LADs and nonLADs were bioinformatically cleaned and regions predicted to be best for hybridization with no off-target binding were kept. Oligonucleotides were synthesized and LAD and nonLAD pools were labeled (panel B). An alternative approach using amplified DamID libraries that were labeled and used as FISH probe do not indicate any specific nuclear organization and look reminsent of DNA counter-staining.

that were deemed inappropriate for in-situ hybridization were removed, and probes were designed in-silico, and selected by temperature and GC content to enable synthesis of 150 base-pair overlapping oligonucleotides. Approximately 144 million probes were synthesized per LAD or nonLAD territory, per chromosome. Chromosome 12 nonLAD regions had less probe (approximately 72 million probes) because there was less genic region on chromosome 12 contained in a nonLAD domain. LADs and nonLADs were then directly labeled with unique colors to enable visual distinction of the two domains.

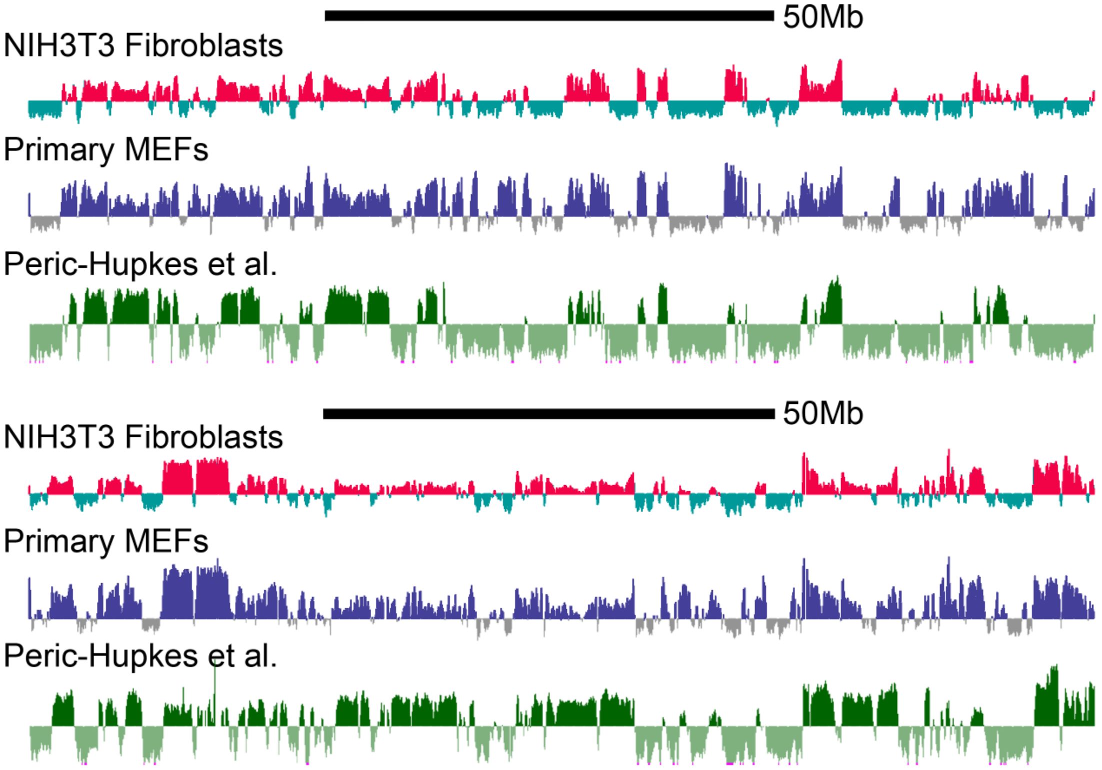


Figure 22 DamID Validation

Initial DamID performed in fibroblasts was compared to DamID profiles in primary mouse embryonic fibroblasts (MEFs) and publically available MEF data . The trends for chromosome 11 (top) and chromosome 12 (bottom) confirm reproducibility of technique and consistency within a single cell type.

These LAD and nonLAD probes for chromosomes 11 and 12 were hybridized in early pass E13.5-14 primary murine embryonic fibroblasts (MEFs) using a 3D fluorescence in-situ hybridization protocol to preserve 3D-organization of nuclei. DamID was performed on these early pass MEFs and compared to the previously published fibroblast data by our group and Peric-Hupkes et al, and general signals for Chromosomes 11 and Chromosomes 12 are the same (Figure 22). The probes applied to these early-pass, 3D, intact nuclei, reveal spatial segregation of the majority of the volume of the LAD and nonLAD domains and their clear organization in interphase nuclei (Figure 23). We observe this strict organization in almost all nuclei with positive hybridization signal.

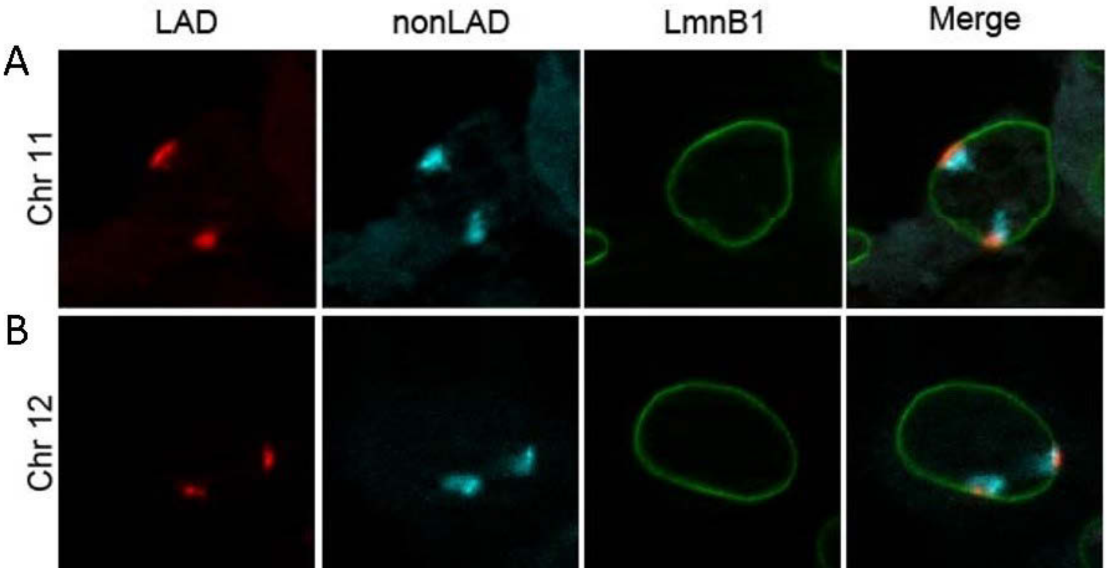


Figure 23 Novel Oligonucleotide FISH probes in Primary MEFs

FISH probes in single wildtype MEF nuclei reveals chromosome organization and the presence of LAD and nonLAD subdomains for both chromosome 11 (panel A), and chromosome 12 (panel B).

In order to determine organization relative to the nuclear periphery, peak lamin signal was designated the 'zero' point and signal intensities for LaminB1 signals, LADs and nonLADs were measured and plotted per chromosome territory in each diploid cell. For all cells, measurements were acquired by observing medial planes and determining pixel distances of each chromosomal sub-territory in relation to laminB1 staining (Figure 24A). Territories were chosen for measurement if they were in the most medial planes, in intact diploid nuclei, and were proximal to the lamina.

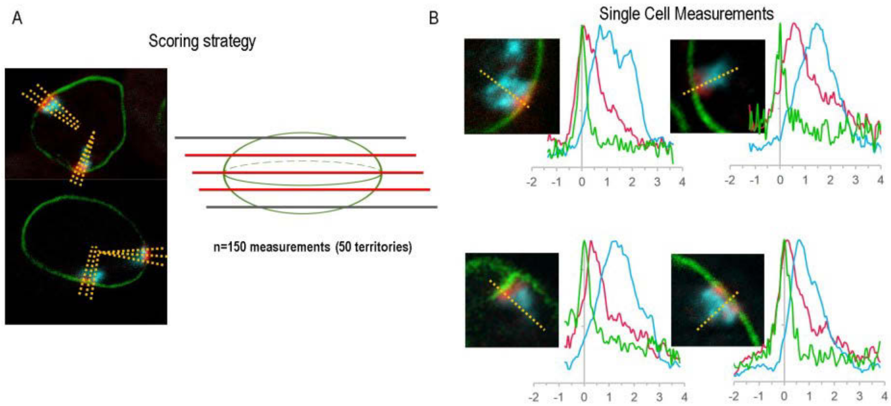


Figure 24 Scoring Strategy

For each territory, three paths (yellow dotten lines) are chosen to measure in the most medial plate (red lines) (panel A) Examples of signal intensities at each point across the line (where laminB1 is set to 0) are shown in panel B. Curves are normalized to 100% signal intensity.

After obtaining individual profiles, the data for each chromosome (Chromosomes 11 and 12, separately) were aggregated to indicate population profiles for organization. When looking at distance measurements from the lamina (defined by LaminB1 staining) through the chromosome territory, the main body of these two territories segregate and the LAD regions are preferentially close to the nuclear periphery, as is seen in the single cell. We observe some overlap of the LAD and nonLAD regions, but note that in every case the signal from the nonLAD regions do not overlap the LaminB1 profiles and preferentially stay away (Figure 23b, Figure 25A, individual measurements Appendix A.8). We expected some overlap between the territories because our probe design did not include any buffer space between LAD and nonLAD coordinates, and the limit of resolution of light

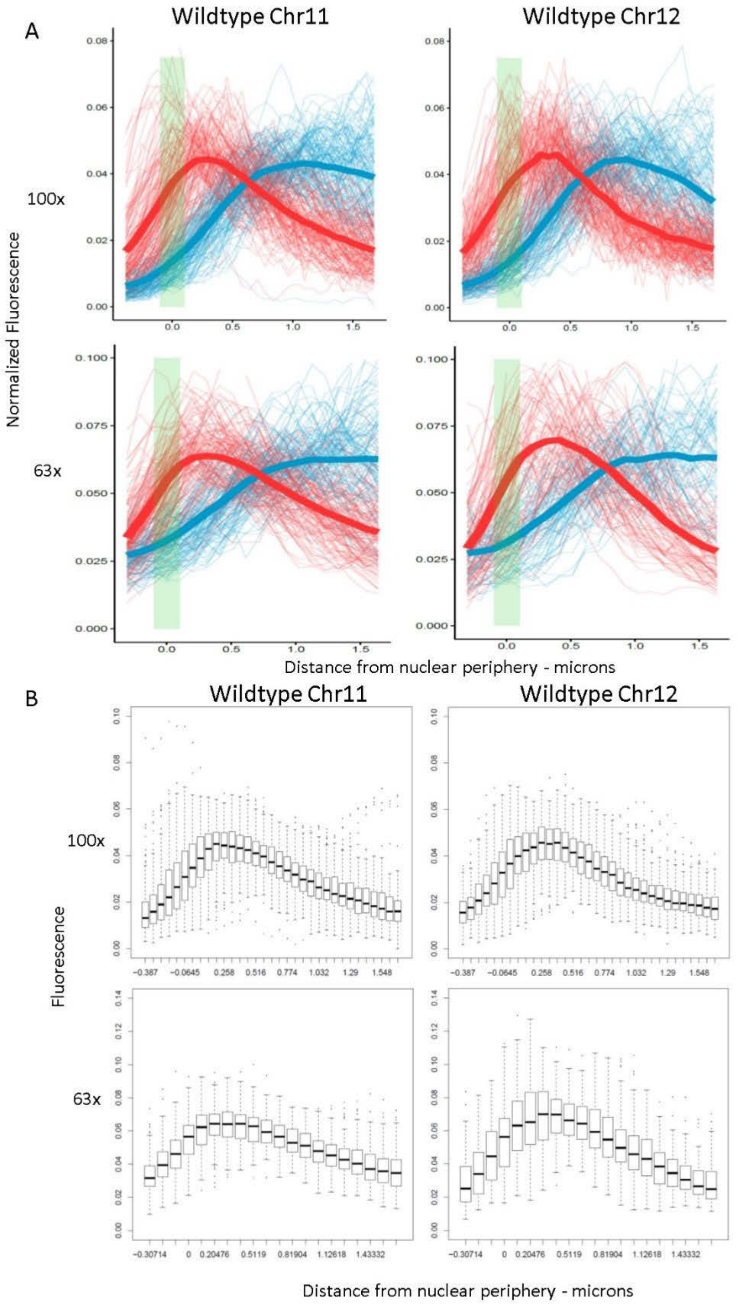


Figure 25 Wildtype LAD Organization and Scoring

Continuous measurements for Chromosome 11 and 12 at 100x and 63x (panel A, top and bottom respectively) plotted to show the distributions of the LaminB1 (green) LAD (red) and nonLAD (cyan) signals. Panel B shows the distribution of the LAD regions in Chromosome 11 (left) 12 (right), at 100x and 63x magnifications (top and bottom). The distributions are not significantly different between conditions.

microscopy is such that we cannot resolve such small spatial differences. We imaged wildtype cells for chromosome 11 and chromosome 12 at 63x objective magnification to maximize data collection, but also turned to 100x objective magnification to more precisely image the LAD and nonLAD domains, and the distributions at both magnifications are identical (Figure 25).

An interesting observation is the apparent sizes of the LAD and nonLAD sub-territories. 3D image analysis shows that the chromosome 11 nonLAD sub-chromosomal territory occupies an average region of 12.3 um^{3} within the nuclear volume, whereas the LAD sub-territory is 7.71um^{3}, which on linear chromosome the LADs cover 26.1% more of the chromosome than nonLAD regions (Figure 21, 26). Chromosome 12 is more compacted with the average territories measuring at 7.8um^{3} for nonLAD and 4.3 um^{3} for the LAD region, but the LADs cover 157% more of the chromosome than nonLADs. These measurements describe a higher level of compaction of LAD domains, which agrees with the observed increase of heterochromatin/electron dense material at the nuclear periphery.

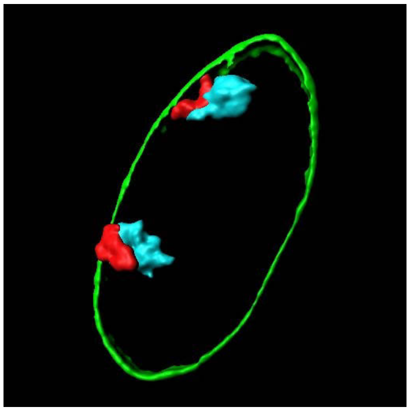


Figure 26 3D rendering of LAD and nonLAD domains

3D volumes of LAD and nonLADs hybridized in primary MEFswere reconstructed using Imaris Images were obtained at 100x objective magnification.

The hybridization and evaluation of the LAD and nonLAD domains were all done in early-pass primary murine embryonic fibroblasts. Extended subculturing of the cells (more than 6 passes) leads to polyploidy and disruptions of nuclear architecture, therefore it was important to maintain a culture that most closely matches the *in vivo* tissue it came from by limiting the time in culture.

4.3 Discovery of the Peripheral Zone

Most strikingly, the majority of LADs are clearly constrained to the most peripheral region of the nucleus in interphase as can be seen in both the individual measurements and population distribution (Figure 25, Appendix A.8). The majority of the LAD signal is contained within a region that extends to approximately 0.6uM from peak lamina signal. We define this region where LADs are concentrated as the peripheral zone. In contrast to a previous report suggesting that LADs identified by DamID only associate with the lamina approximately 30% of the time, we observe a stable association of the majority of LAD signal within this peripheral zone. In addition, it is striking that for two different chromosomes, the peripheral zone appears to display identical distribution, suggesting a generally constant architecture across wildtype cells of this compartment. While our own studies indicate that there is chromatin dynamics and movement within the peripheral zone (Wong et al, in preparation), we see no evidence of the majority of DamID identified LADs displaying the type of variance of association indicated by these previous studies. We note that we are not observing the dynamics of individual LAD association with the lamina proteins, and it is likely that specific regions are able to move closer or come into molecular contact with the nuclear periphery and move away in a stochastic fashion, but our data indicates that these movements are generally restricted to the peripheral zone.

As we have measurements for both chromosome 11 and chromosome 12, we notice that the LaminB1 profiles for both chromosomes overlap indicating that this rigid structure is approximately the same size in all the cells measured and further validating our measurement technique (Figure 27). An outstanding observation can be seen with the LAD profiles between Chromosomes 11 and 12 in that they directly overlap, indicating that peripheral zone is consistent across chromosome territories and is likely a stable compartment. The nonLADs, however, do not have a specific region they occupy and the variation of each individual nonLAD sub-territory is very high. This is an interesting result that further supports that the LADs are constrained or restrained in a way that the nonLADs are not.

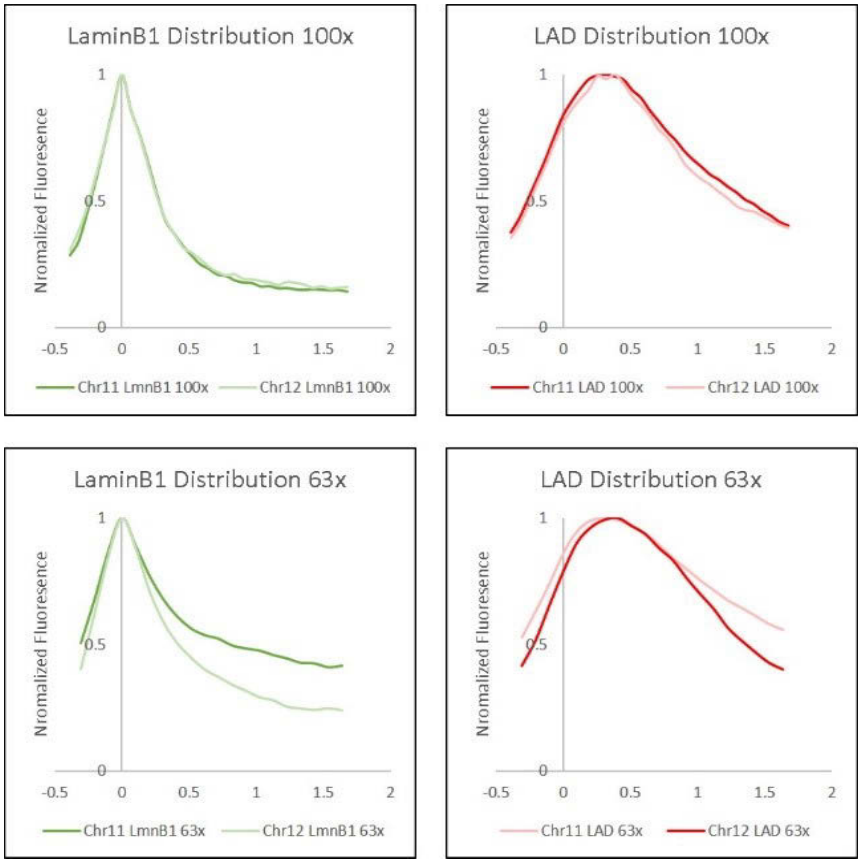


Figure 27 LAD and LaminB1 Overlap

Plots of LaminB1 signals and LAD signals at each magnification (100x, top, 63x, bottom) shows the distributions are the same.

Additionally, we notice that all the LAD domains on a single chromosome aggregate to one distinct chromosome sub-domain within the peripheral zone (Figures 23 and 26). These self-associating LAD domains (saLADs) exist as distinct regions of chromatin that are lamina-proximal and separate from the nonLAD domains. The banding patterns of the chromosomes suggests that LADs and nonLADs are interspersed as they are on the linear genome. The oligonucleotide paints are able to demonstrate the folding and higher organization of the chromosome by highlighting this unique configuration and segregation of the two domains.

4.4 Variable LADs are no longer restricted to the peripheral zone in permissive cell types

Of particular interest to our group is the murine immunoglobulin heavy chain locus, which clearly resides in a LAD on chromosome 12 in murine fibroblasts (Figure 5, 6, 12a, and 28b). Previous work on the *IgH* locus has demonstrated that the *IgH* locus is dynamically positioned based on cell type, and this variable positioning coincides with active transcription and lineage progression.(Reddy et al. 2008; Harr et al. 2015) Current literature supports these observations of variable LAD patterning across cell types. Our own work studying LAD dynamics, described in Chapter 2 and Harr et al, also contributes to this body of work and specifically highlights a number of other developmental gene-containing variable LADs. These regions not only demonstrate differential molecular contact with the nuclear periphery, but also show a change in cytological position when visualizing individual loci. We term regions of chromatin that show differential patterns of association at the lamina across cell types “variable LAD” regions, or “vLADs”, to reflect the dynamics of chromatin association without making assumptions of function. LADs that do not vary between cell types, or are common across maps, we refer to as "common LADs" or "cLADs". We emphasize the use of the word 'common' because without further study of all possible cell types, we cannot ascribe function to these LAD regions, and they may be vLADs when comparing different systems (reviewed (Luperchio, Wong, and Reddy 2014)). In the case of the *IgH* locus, which is a nonLAD in pro-B cells as defined by DamID, but, in fibroblast cells, the DamID maps indicate it is in a LAD in fibroblasts and therefore constitutes a vLAD (Figure 28b).

Upon the discovery of the peripheral zone and the utility of the novel oligo probes in studying LAD and nonLAD compartments, we asked if we can detect these variably associating regions and visualize their escape from the peripheral zone in divergent cell types. To do this, we hybridized our chromosomal sub-compartment probes, which were designed using fibroblast LAD and nonLAD data, to pro-B cells, where we already have established differential molecular LAD maps (Harr et al. 2015). Upon hybridization and analysis, we observe an expansion of the LAD profile past the peripheral zone into the interior of the nucleus when looking at both individual measurements and the population of cells, indicating that LADs do move out of the peripheral zone. Since we know the *IgH* locus moves into the nuclear interior in pro-B cells, we chose to visualize the *IgH* locus within the LAD domain by combining a BAC probe specific for the *IgH* locus along with the sub-chromosomal paints. This experiment results in clear visualization of the *IgH* vLAD movement out of the peripheral zone and into the nuclear interior. (Figure 28a). Measurements of individual cells show a profile of where the LADs and nonLADs reside in this cell

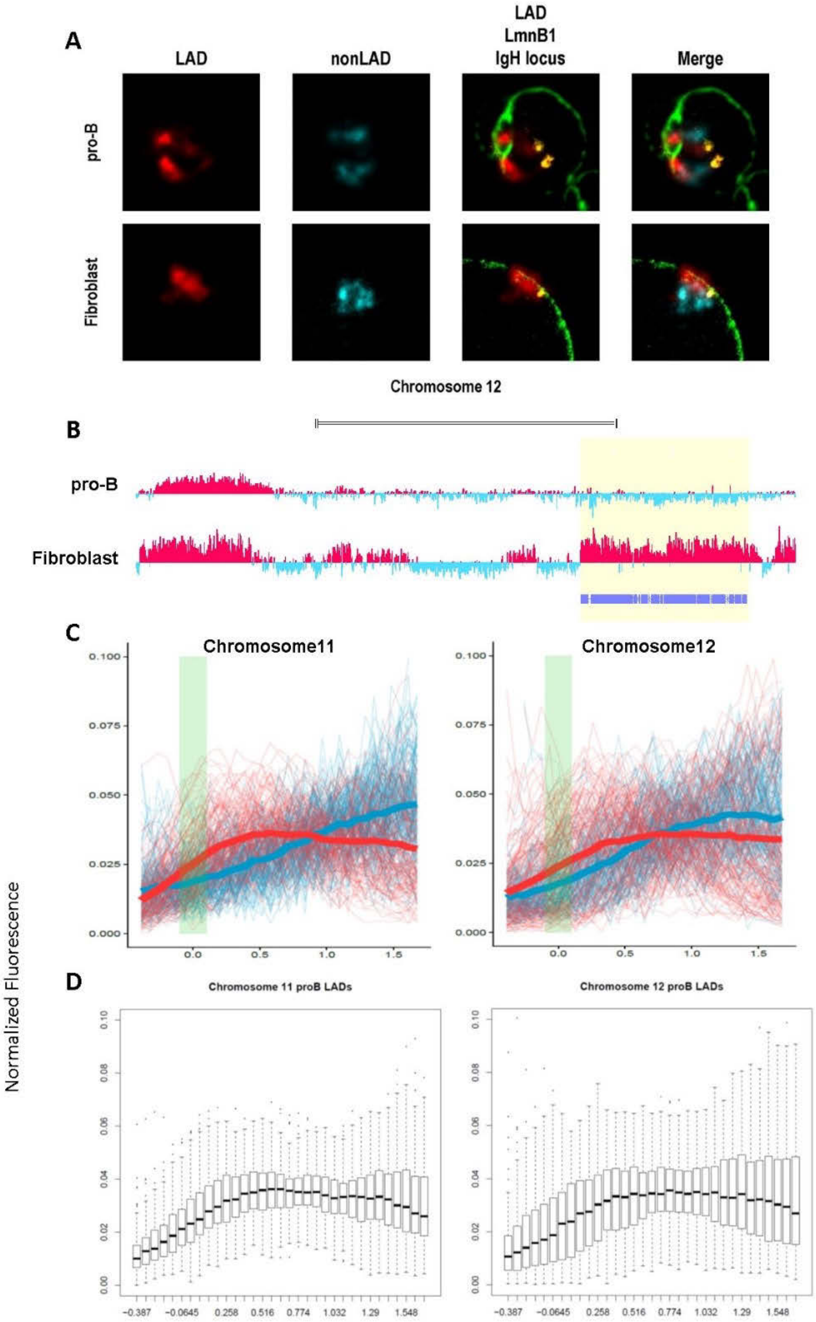


Figure 28 pro-B cell profiles of LAD and nonLAD domains

Novel oligonucleotide probes show organization of LADs (red) and nonLADs (cyan) in fibroblasts (panel A, bottom) and pro-B cells (panel A, top). The IgH locus is centrally disposed in pro-B cells and in a vLAD (IgH in yellow, merge with red, panel A). DamID data in pro-B and fibroblast cells show the IgH is in a vLAD (panel B). Plots of individual measurements show LADs reach into the nuclear interior (panel C) and may be similar to nonLAD regions. The distribution of LADs signals for chr11 and chr12 show an increase of incidence of signals in the nuclear interior

type, and there is a peak of 'LAD' signal where the *IgH* signal peaks and also in other parts of the nuclear interior, indicating the repositioning of variable LAD domains and genome reorganization (Figure 28c). Here we clearly demonstrate the ability to visualize vLAD movement out of the peripheral zone. It is noteworthy that the bulk of the LAD signal still remains within the peripheral zone, which likely represents the cLAD portion of the chromosome, and the retention of some LAD signal in the peripheral zone and the movement of some signal to the nuclear interior changes the saLAD organization. It will be interesting to see in future studies how consistent the size of the peripheral zone and the saLAD domain is in tissue and species specific models, and if this region is a stable compartment shared between multiple cell types.

4.5 LADs, chromosome structure, epigenome stability and nuclear integrity

Recent studies have focused on the identity of this peripherally associating chromatin, and how LAD domains relate with the epigenome (Peric-Hupkes et al. 2010; Meuleman et al. 2013; Guelen et al. 2008; Kind et al. 2013). Initial studies have correlated large domains of H3K9me2 to LAD regions noting an 80% overlap, though in different cell types (Wen et al. 2009). Other studies have investigated the epigenetic signatures of LADs either through bioinformatics and chromosome modeling (Guelen et al. 2008; Filion et al. 2010; Hu et al. 2013), developmental studies examining accumulation of epigenetic marks during LAD formation (Towbin et al. 2012), chromatin signatures as specific loci (Bian et al. 2013) and directed molecular studies aiming to study *de novo* LAD formation, chromatin signatures and molecular cues (Harr et al. 2015; Bian et al. 2013). All of these studies together suggest that LAD chromatin does in fact have a special epigenetic signature, yet the exact profiles have yet to be fully elucidated. The work mentioned above and from our lab have suggested that LAD bodies are marked with H3K9me2/3, the borders are enriched in H3K27me3, and that the accumulation of these histone modifications contribute mechanistically to LAD formation and maintenance.

4.5.1 The epigenome and LAD organization

These studies have highlighted a relationship between local chromatin state and LAD formation and maintenance, but have focused on individual LADs. Next, we wanted to experimentally address the question of whether globally LADs, and sub-chromosomal architecture are affected by epigenetic perturbation. Choosing drugs that have been established in the literature to cause specific epigenetic perturbations, we treated cells to disrupt their normal epigenetic state, and then assessed their nuclear organization using the LAD and nonLAD oligo probes (Maison et al. 2002; A. Taddei et al. 2001; Angela Taddei et al. 2005; Kubicek et al. 2007; Ostrup et al. 2014). We treated primary MEFs with TSA, an HDAC inhibitor that prevents histone deacetylation, Bix01294 a histone methyltransferase inhibitor which targets GLP and G9a and therefore inhibits H3K9me2, and DZNep which decreases H3K27me3 through its activity as S-adenosylhomocysteine synthesis inhibitor and a histone methyltransferase EZH2 inhibitor. (Figure 30 C)

TSA has previously been shown to disrupt normal associations at the nuclear periphery, and rearrange portions of the genome as determined by microscopy (Maison et al. 2002; Taddei et al. 2001; Taddei et al. 2005). When early-pass primary cells were treated for 24-48 hours with TSA, we see global disruption of the chromosome territories. The LAD regions are able to move out the peripheral zone though a portion of the LADs remain at the lamina, and the nonLAD and LAD regions, which are normally well segregated, comingle. It does however appear that some subdomains within each territory remain, as indicated by discrete puncta of LAD and nonLAD signal (Figure 29a) The individual cell to cell variation of the LAD territory across the nucleus is high, unlike in the wildtype population. This variation can be seen in the plots of the individual measurements especially outside of the peripheral zone (Figure 29b). Some cells retain some LAD association at the periphery while the LAD regions extend into the nuclear interior, some cells maintain the wildtype configuration, and some cells show a random or stochastic distribution of LADs across the nucleus. Additionally, the distribution of the LAD signal diverges from the wildtype condition where we see an increase of signal at the nuclear interior, and indicates that the LAD chromatin is no longer restricted to the peripheral zone (Figure 29b and c).

While we are able to visualize reorganization of the LAD and nonLAD domains as well as movement of LAD domains away from the peripheral zone, these are cytological observations and the limit of resolution in microscopy prevents us from making accurate predictions of the molecular associations at the periphery in this cell state. To identify chromatin-lamina interactions in TSA-treated early pass primary MEFs, we performed DamID on TSA treated early pass MEFs (Figure 30).

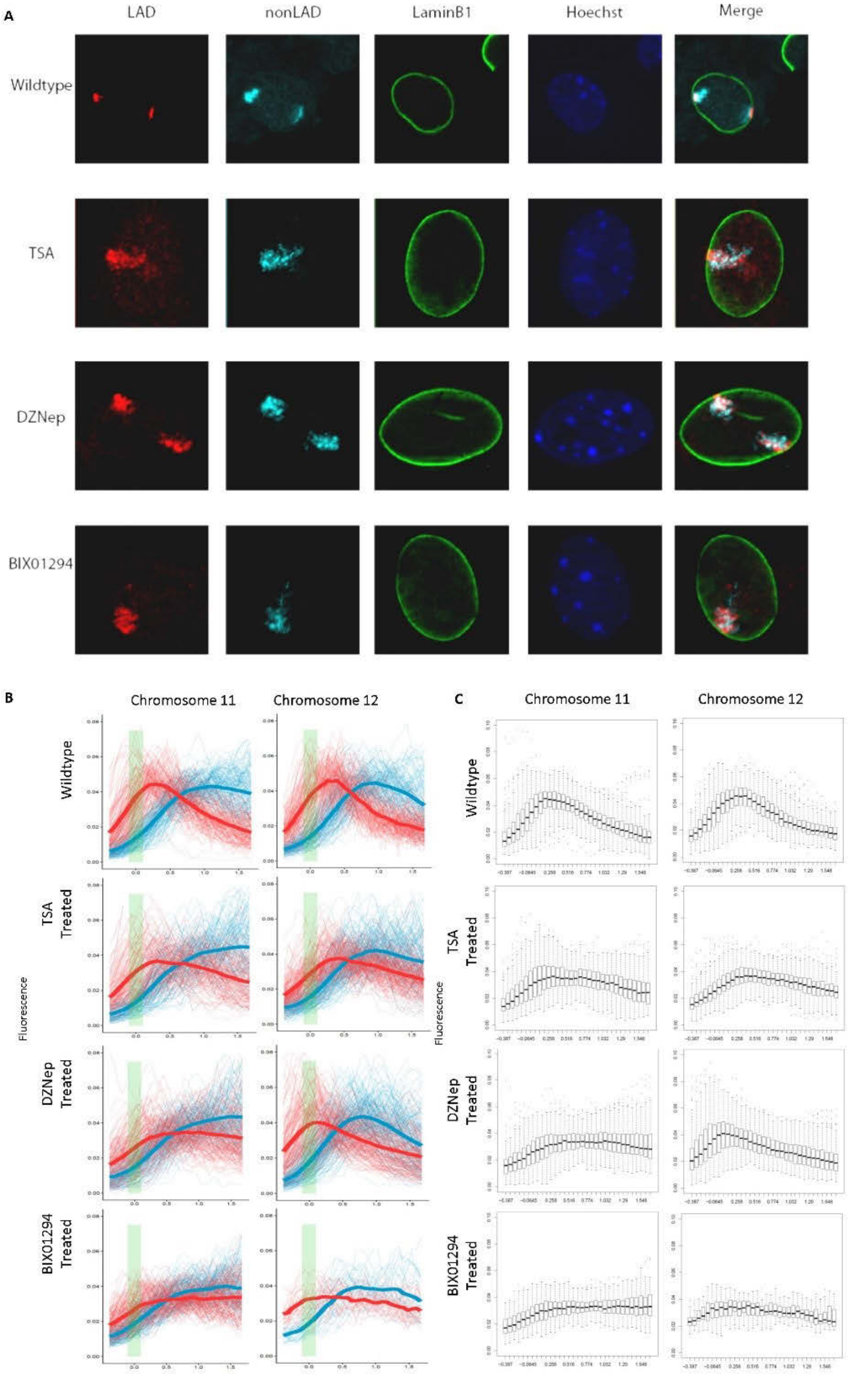
Cells were TSA treated prior to the introduction of the DamID construct to ensure the inclusion of only TSA affected cells. Comparing genome-wide data between the wildtype MEF DamID to TSA MEF DamID, we see mild but significant differences in the two data sets. We notice a loss of LADs at some genomic locations, but we do not detect a global disruption of the LAD profiles as the cytological data would suggest (Figure 30, Appendix A6). We do also note a lower Dam-LaminB1/Dam log2 ratio score in many regions across the genome-wide molecular contact map which could potentially indicate weaker interactions of chromatin with the lamina, but cannot conclude that this effect is because of decreased frequency of association with the periphery or if it is variability due to the individual experiment. The largely similar genomic profile of LaminB1 association to the wildtype or vehicle-only treatment is likely an effect of two caveats of the DamID experiment: The molecular contact maps are based on the population of the cells and reflect all positive interactions with the nuclear periphery and cannot describe individual variation, and; DamID is a simple proximity measure. All regions that come close enough to the lamina-tethered Dam methylase will become GATC adenine-methylated, including stochastically associating regions. With the disruption we observe using the domain paints, the fact that there is a lot of individual cell-to-cell variation complicates the analysis of the DamID data, and leads us to conclude that DamID is not a sufficient technique to measure this type of genome organization or disorganization.

After broadly disrupting the epigenome with introduction of the HDAC inhibitor TSA, we attempted to specifically alter H3K9me2 and H3K27me3 profiles across the genome to study the effects on LADs (Figure 29). Upon treatment with

BIX01294 (reduces H3K9me2 through G9a inhibition, Figure 30c) and hybridization

Figure 29 Epigenetic Perturbation and Sub-chromosomal Architecture

LADs and nonLADs are visualized in wildtype, TSA treated, DZNep treated and BIX01294 treated cells. (panel A). Individual measurements (panel B) show distributions of LAD (red) and nonLADs (blue) relative to laminB1 (green). LADs lose their normal distributions and are no longer concentrated in the peripheral zone (panel C)



of the domain paints, we see disruption of the chromosome territories with some

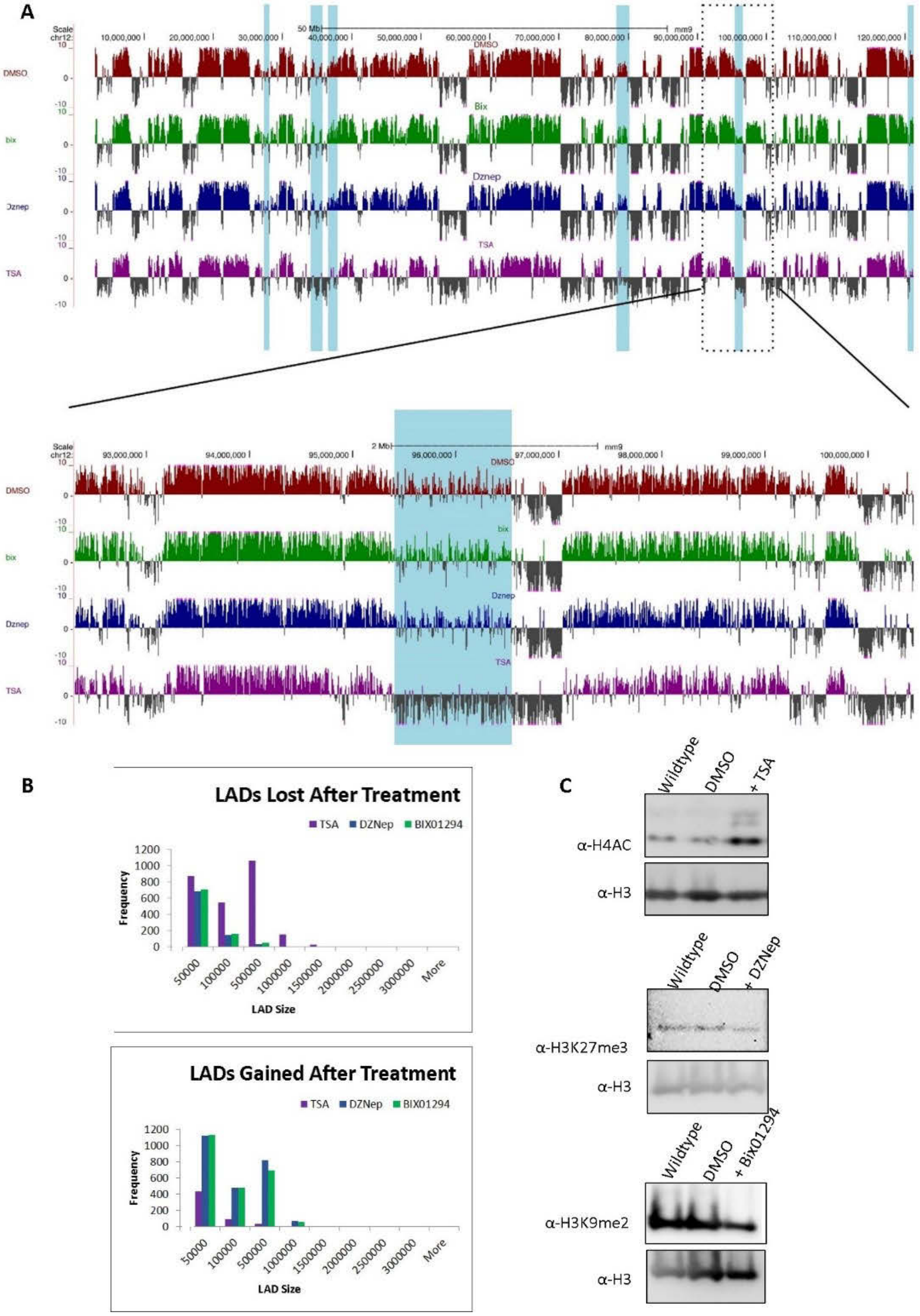


Figure 30 Drug Treatment in DamID

DamID maps for DMSO treatment (red) and drug treatments in MEFs are shown, Bix01294 in green, DZNep in blue and TSA treatment in purple. Light blue regions highlighted show differences in LAD signals, differences are only in TSA treatment. (B) shows distribution of LADs gained and lost compared to DMSO treatment. Panel C shows western blotting of target histone modifications after drug treatment.

retention of LADs in the peripheral zone, but also that the LAD and nonLAD territories comingle. DZNep (H3K27me3 reducer through EZH2 inhibition) treatment also results in disruption and reorganization of chromosomes 11 and 12, although each are affected differently. Chromosome 12 LAD distribution across the nucleus is less affected than chromosome 11, which we hypothesize is because of the increased level of compaction of chromosome 12 (Figure 29c). While we have not tested this, we hypothesize that the mechanism directing this compaction and retention at the nuclear periphery is unaffected by H3K27me3. DamID treatment and sequencing of both DZNep and BIX01294 treated MEFs was performed in parallel with the TSA treatment, and in an examination of the population-based molecular contact maps, it was difficult to visually detect any differences in LAD profiles not reflective of the individual variation observed (Figure 29a and 30a). The LADetector is able to detect some perturbations relative to DMSO treatment and the disruption of the BIX01294 and DZNep treatment look similar in terms of LAD sizes gained and lost (Figure 30 and Appendix A6 and A7). The numbers and distribution of LADs lost in the DZNep and BIX01294 treatment are similar to the expected changes when comparing replicate wildtype or control DamID profiles, but the data suggests there is a small increase in gained LADs. From the overall visual examination of the DamID maps after TSA treatment (as described above) we can see the loss of large LAD domains compared to the wildtype profiles and applying the LADetector, we find there are many large LADs lost and very few LADs gained relative to the other drug treatments. Comparing the DamID profiles of the BIX01294, DZNep and TSA treated cells, the data suggests that the indicating that the TSA treatment affects genome organization on a larger scale and more consistently across the population (because DamID is reflective of the organization of the population of cells) than DZNep and BIX01294 treatment.

4.5.2 Nuclear integrity and LAD organization

In addition to testing the relationship of the epigenome and chromosome organization, we also asked how nuclear integrity may impact chromosome and LAD domain organization. The lamina proteins, which govern nuclear integrity in cooperation with other structural proteins, have been implicated in diseases that may involve the genome and epigenome and can lead to a loss of peripheral heterochromatin (Wong, Luperchio, and Reddy 2014). To test the effect of nuclear

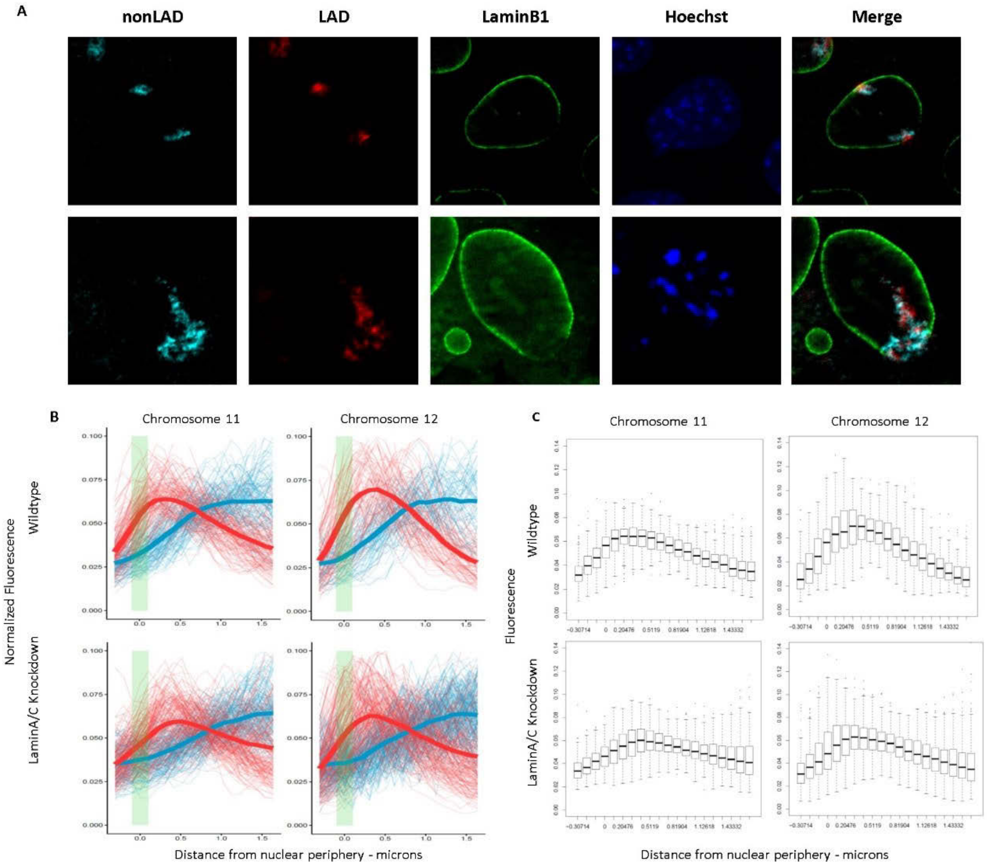
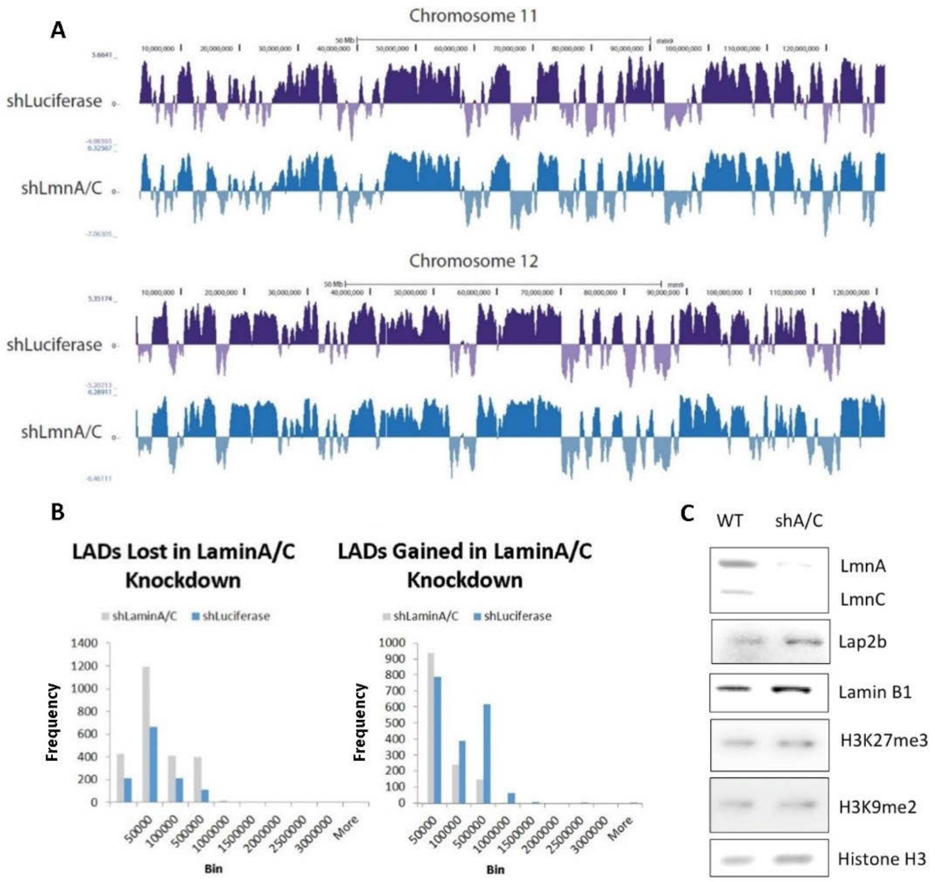


Figure 31 LaminA/C knockdown

FISH signals in wildtype and LaminA/C knockdown (panel A) show the disorganization of chromosome sub-territories after LaminA/C knockdown. Measurements of wildtype and LaminA/C chromsomes 11 and 12 are plotted (panel B). Distributions of LADs for are plotted in panel C.

Figure 32 DamID-seq in LaminA/C knockdown

DamID data for shLuciferase (dark blue) vs LaminA/C knockdown (shLmnA/C, light blue) is displayed for Chromosome 11 and 12. Distribution of LADs gained and lost are plotted in panel B.Western data (panel C) profiling knockdown of LaminA/C and epigenetic marks.



integrity on chromosome organization, we knocked down LaminA/C, two proteins that are part of the nuclear lamina network and that we have previously shown are important for maintenance of a single LAD at the nuclear periphery. (Figure 32c, Harr et al. 2015) Knockdown of LaminA/C leads to a disruption of the chromosome organization, reminiscent of what we observe with disrupting the epigenome using drug treatments, where the segregation of the LADs and nonLADs is no longer evident and the saLAD domain is dispersed (Figure 31a). DamID analysis of the LaminA/C knockdown also shows no significant deviations from the wildtype patterning, and changes in LADs observed are what we expect for normal experiment-to-experiment variation (Figure 32a and b). Interestingly, after LaminA/C Knockdown in primary MEFs, we see no changes to the epigenome such as decrease of histone modification levels that may explain the disruption of the 3D organization (Figure 32c). The disrupted 3D genome organization and de-establishment of LADs is an early phenotype that immediately follows LaminA/C knockdown.

4.6 The relationship between LADs and higher order chromatin structure

The creation and usage of these novel oligonucleotide paints reveal chromosome-wide LAD and nonLAD profiles in single cells, and also allow us to begin to understand how LADs fit into higher order chromatin structure. Notably, HiC data suggests the presence of two distinct compartments, the “A” compartment, which is ‘active’ and has been associated with non-LAD regions, and the “B” compartment, which has been associated with LADs.(Vieux-Rochas et al. 2015) This simplistic view of higher order genome organization matches our observation that chromosomes are organized in two distinct domains based on LADs and nonLADs. A number of reports using HiC technology to probe inter- and intra-chromosomal interactions have uncovered the existence of *cis* regions of chromosomes that preferentially self-associate and are distinct from other domains of the same type (Dixon et al. 2012; Sexton et al. 2012). These sub-nuclear domains have been called topologically associating domains (TADs) and it was noted that many TAD boundaries overlap LAD boundaries, but not in all cases.(Dixon et al. 2012) We noted that upon disruption of the chromosome territories as a result of insult to the epigenome or nuclear integrity, we see a disassociation of the LAD region from the nuclear periphery and also from each other (the saLAD domains are disrupted). We wanted to investigate if LADs in fact do associate over long distances. Due to the lack of MEF Hi-C data, we were unable to compare Hi-C and DamID data in MEFs, so we turned to our genome-wide pre-pro-B DamID data (LADs from Chapter 3) and publically available Hi-C data from (Lin et al. 2012) to ask if these cells display long-range interaction. By aligning the DNA-DNA long range interaction maps (Hi-C) and LAD domains (DamID), we can see that there are in fact long-range interactions between LAD domains, and LAD and nonLAD domains do not interact (Figure 33).

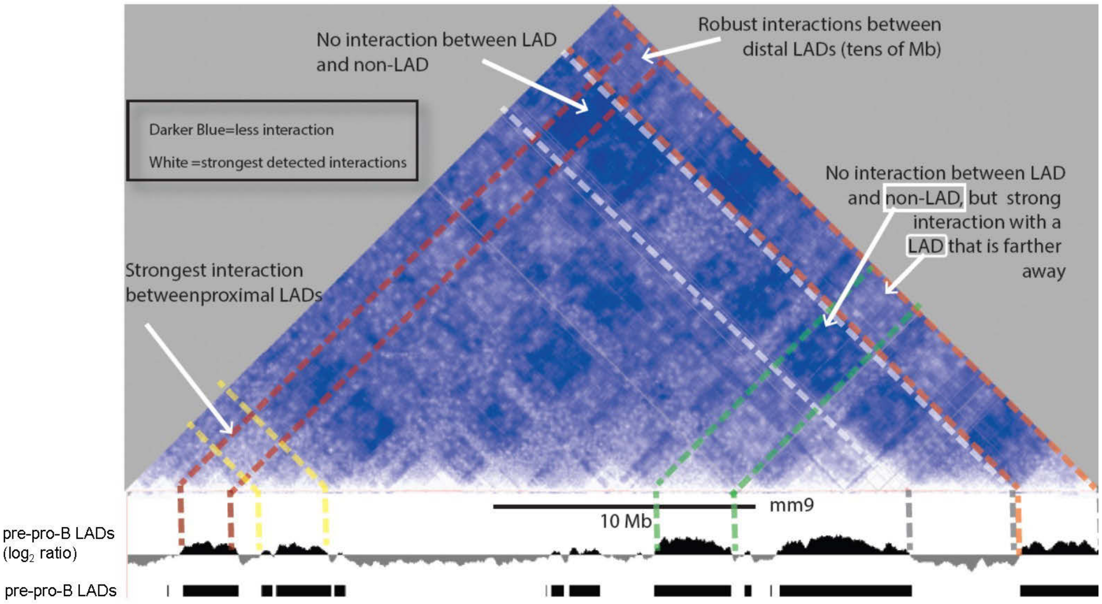


Figure 33 HI-C and LAD data from pre-pro-B cells

LADs self associate over long distances. Dotted lines show LAD or nonLAD domains. Arrows point to intersections which measure interaction level

Upon in-depth visual comparison of our LAD data and TADs, we agree that some TAD boundaries overlap overall LAD borders, but most interestingly, many TAD boundaries overlap with vLAD borders (Figure 34). A close examination of these previously defined TADs shows that the TADs can be divided into smaller increments based on the domainograms, which show a striking overlap with vLAD boundaries (Figure 34). An extensive study on TADs and smaller domains within them (sub-TADs) suggests that the genome could potentially adopt many configurations based on these sub-TADs and associated architectural proteins.(Phillips-Cremins et al. 2013) The discovery of the sub-TADs supports our hypothesis that chromosome organization, with respect to LAD organization, is modular on these intermediate TAD regions, or iTADs (incremental TADs). Our

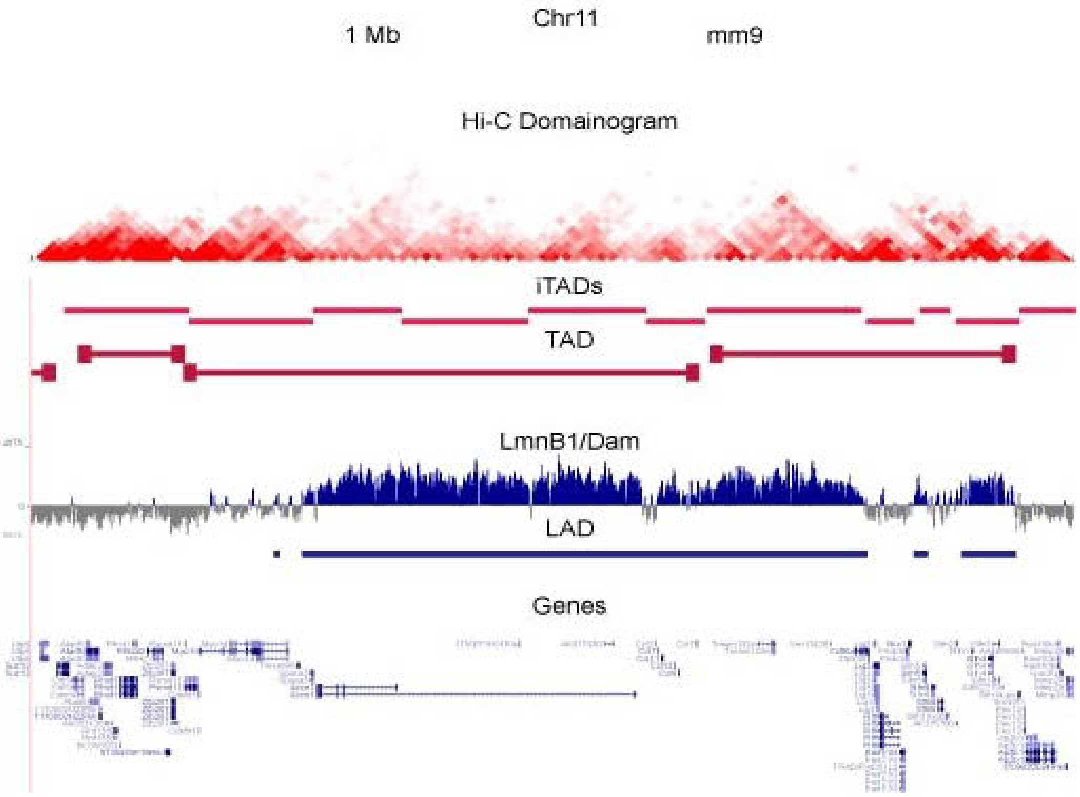


Figure 34 Higher order chromatin structure and LADs

LADs aligned with HiC data reveals discrete units (iTADs) that correspond with LAD borders previous work on vLAD dynamics and patterning across cell types leads us to suggest that the distinct regions over which vLADs occupy are directed by these HiC defined domains. Also, the evidence of the Hi-C ‘closed’ B compartment mentioned previously and the comparison of long-range self-association patterns of LADs (Figure 33 and 34) provides strong evidence that our cytological data demonstrates the existence of saLADs (self-associating LADs) and sub-chromosomal organization based on LAD and non-LAD architecture.

4.7 Discussion

The development of our novel oligonucleotide paints uncovers a previously undiscovered higher-order chromosome organization. The identification of the peripheral zone, or the region of the nucleus where the LADs are restricted, showcases the functional organization of the chromosome, and also agrees with other previously published studies (Yao et al. 2011; Hu et al. 2013). A beautiful study in the literature describes the developmental activation of the MyoD gene after its relocation to the nuclear interior, and the authors found that the necessary transcription factor for gene expression of the MyoD locus, Taf3, is excluded from the nuclear periphery and is retained only in the nuclear interior. (Yao et al. 2011) We suggest that Taf3 is being excluded from the peripheral zone and the LAD domain to allow for sequestration of the MyoD locus in the peripheral zone to prevent gene activation. Additionally one study provided computational models to suggest that chromosomes are organized based on gene density and activity (Hu et al. 2013). These models based on HiC data have suggested a preferred organization and even an enrichment of some chromatin domains for presence of epigenetic marks and lamin association (Hu et al. 2013). Our application of chromosome-wide molecular data to 3D, intact, primary mouse embryonic fibroblast nuclei has allowed us to visualize chromosome organization that other studies have only implied.

Most significantly, we also demonstrate that 3D chromosome organization is dependent on cell state, and can be specifically reorganized during development, or disorganized during disruption of epigenetic and structural integrity. Changes in cellular identity, loss of epigenetic regulation, or increase of nuclear instability contributes to dynamic genome and chromosomal sub-domain reorganization. In the case of disease that impact nuclear integrity (such as progeria), or that impacts epigenetic stability and identity of cells (such as some cancers), it is possible that the chromosome territory is also rearranged. Our novel oligonucleotide paints created and utilized through this work may be able to identify these pathological cell states, and also may be able to identify chromosome disorganization as an early detector since we see disruption of the territories as the first response to cellular perturbation (epigenetic drug treatments or laminA/C knockdown).

4.8 Methods

4.7.1 Cell culture

Primary murine embryonic fibroblast generation and maintenance

Wildtype eight-week-old C57BL/6 mice were bred and embryos were harvested at E13.5. Individual embryos were homogenized using a razor blade, and cells were disassociated in .25% trypsin for 20 minutes 37'C. Cells were pipeted vigorously to establish single cells and then plated in 10cm dishes in a total of 9mLs DMEM hi + 10% FBS+Penicillin/Streptomycin+L-glutamine+non-essential amino acids and labeled as P0. Cells were cultured for no longer than 5 passages before harvesting for experiments.

pro-B cell culture

Ex-vivo expanded Rag2-/- pro-B cells were co-cultured with Op-9 stromal cells in Opti-MEM supplemented with 5%FBS+Penicillin/Streptomycin+L-Glumatine+0.1%Beta-mercaptoethanol and 3ng/mL Il-7.

4.7.2 DamID

DamID was performed as described in Chapter 2 with few modifications. MEFs were purchased from ATCC (CRL-2752) and cultured according to their established protocols, in medium containing DMEM High, 10%FBS, Penicillin/Streptomycin and L-glutamate. DamID was performed using nature protocol method, self-inactivating retroviral constructs pSMGV Dam-V5 (Dam-Only) and pSMGV Dam-V5-LaminB1 (Dam-LaminB1) were used to generate retrovirus using the Platinum-E packaging line (RV-101, Cellbiolabs). Supernatants containing viral particles were collected between 48-72 hours after transfection of the DamID constructs, and collection times were pooled. For Drug treatment, primary fibroblasts were treated with either TSA, BIX01294, DZNep or DMSO (vehicle) for 18-24 hours prior to incubation with DamID virus. MEFs were incubated overnight with either Dam-only or Dam-LAMINB1 viral supernatant and 4ug polybrene. Pro-B cells were spinfected for 2 hours at 2000g, recovered for 2 hours. Cells were allowed to expand for 2-4 days then pelleted for harvest. Fibroblast cells were trypsinized from the plate and DNA was harvested using QIAGEN DNA Mini kit, precipitated and resuspended to 1ug/ul. .5-2.5ug of this genomic DNA was digested overnight with restriction enzyme DPN1 (R0176, NEB) and then heat-killed for 20 minutes at 80’C. Samples were cooled, then double stranded adapters of annealed oligonucleotides AdRt (5′-CTAATACGACTCACTATAGGGCAGCGTGGTCGCGGCCGAGGA-3′) (IDT) and

AdRb (5′-TCCTCGGCCG-3′) (IDT) were ligated overnight with DPN1 digested fragments (T4 DNA Ligase 799009 Roche. After incubation the ligation was heat-killed at 65'C for 10 minutes, samples were cooled and then digested with DPNII for one hour at 37'C (R0543 NEB). This material was normalized using initial gDNA concentrations then amplified in ligation-mediated PCR using AdR_PCR oligo as primer (5′-GGTCGCGGCCGAGGATC-3′) (IDT) and Advantage cDNA polymerase mix (639105 Clontech). Amplicons were electrophoresed in 1% agarose gel to check size distribution of library and then column purified (QIAquick PCR Purification QIAGEN). Once purified, material was checked for LAD enrichment using controls specific to an internal Innunoglobulin heavy chain *Igh* LAD region (*J558 1*, 5′-AGTGCAGGGCTCACAGAAAA-3′, and *J558 12*, 5′-CAGCTCCATCCCATGGTTAGA-3′) for validation prior to microarray hybridization and/or sequencing.

4.7.3 Probe Design and preparation

LAD and nonLAD chromosome-wide probes

LADs were defined through the LADetector algorithm, and complimentary regions to Chromosomes 11 and 12 were defined as nonLADs. Centromeres were excluded, and LAD and nonLADs were repeat masked. Probes were selected in silico based on TM and GC content, and those with high homology to off target loci were specifically removed. 150 base pair oligos were chemically synthesized using proprietary Agilent technology and probes were labeled in either Cy3 or Cy5 dyes using the Genomic DNA ULS Labeling Kit (Agilent, 5190-0419). 40ng of LAD and nonLAD probes were combined with hybridization solution (10% dextran sulfate, 50% formamide, and 2× SSC) then denatured at 98'C for 5 minutes and preannealed at 37'C.

IgH BAC probe

CT7562A21 probe specific for the *IgH* locus was labeled with Dig during nick translation (DIG-NICK TranslationMix, Roche 11745816910) followed by column purification (QIAquick PCR Purification QIAGEN). BAC probes were included in the hybridization solution with blocking DNAs (9 µg salmon sperm DNA, 6 µg placental DNA, 3ug COT-1 DNA) and hybridized as described.

4.7.4 Fluorescence in situ hybridization and immunofluorescence

Fibroblast cells were plated on poly-L-lysine coated slides overnight. pro-B cells were prepared similarly, but plated on slides for 15-30 minutes in a humid chamber at 37’C and hypotonically treated in 0.3XPBS for 30 seconds. Cells on slides were fixed in 4%PFA/1XPBS for 10-15 minutes, then washed 3 times 5 minutes each wash in 1XPBS. After fixation and washing, slides were permeabilized in 0.5% TritonX-100/0.5% Saponin for 15 minutes. Slides were washed 3 times 5 minutes each wash in 1XPBS, then acid treated in 0.1N hydrochloric acid. Slides were placed directly in 20% glycerol/1XPBS and then incubated overnight at 4’C. After soaking in glycerol, slides were frozen in liquid nitrogen and thawed 4 times. Slides were then RNAse treated (100 µg/ml) for 15 min in 2× SSC at room temperature in a humidified chamber. Slides were hybridized by washing in 70% formamide/2x SSC at 76°C for 3 min, then 50% formamide/2x SSC at 76°C for 1 min, and then overnight at 37°C in a humidified chamber. After overnight incubation, slides were washed three times in 50% formamide/2× SSC at 47°C, three times with 63°C 0.2× SSC, one time with 2× SSC, and then two times with PBS before blocking with 4% BSA in PBS for 30 min in a humidified chamber. Slides were then incubated with primary antibody (α-LaminB1 [1:100; Santa Cruz]) in blocking medium overnight at 4°C. Slides were washed three times with PBS/0.05% Triton X-100 and then incubated with secondary antibody in blocking medium (1:100; DyLight 488, Jackson ImmunoResearch, West Grove, PA) for 1 hr at room temperature. Post incubation, slides were washed three times with PBS + 0.05% Triton X-100, and then DNA counterstained with 1 µg/ml Hoechst. Slides were then washed, mounted with SlowFade Gold (Life Technologies).

4.7.5 DamID-seq

Library Preparation

Post-DamID amplified material was randomized by performing an end repair reaction followed by a ligation and sonication.-.5-5ug of column purified (QIAquick PCR Purification Kit: Qiagen, 28104) DamID material was end repaired using the NEBNext End Repair Module (NEB E6050S) following manufacturer's recommendations.-Subsequently, the end-repaired DNA was purified, again, using the QIAquick PCR Purification Kit (Qiagen, 28104).-1ug of the resulting DNA was then ligated in a volume of 20uL with 1ul of T4 DNA ligase (Roche, 10799009001) at 16'- The ligation mix was topped up to 200ul using ddH2O.-Sonication was carried out using the Bioruptor® UCD-200 at high power, 30s on, 30s off for 1 hour in a 1.5ml DNA lo-bind microfuge tube (Eppendorf).-The DNA was then transferred to 1.5 ml TPX tubes (Diagenode C30010010-1000) and sonicated for 4 rounds of 10 min long sonication with settings of high power, 30s on and 30s off.-The DNA was transferred to new TPX tubes after each round to prevent etching of the TPX plastic. The sonication procedure should yield DNA sizes ranging from 100-200 bp. After sonication, the DNA was precipitated by adding 20ul of 3M sodium acetate pH5.5, 500ul ethanol and supplemented with 3ul of glycogen (molecular biology grade, 20mg/ml stock) and kept at -80'C for at least 2 hours. The DNA mix was centrifuged at full speed for 10 min to pellet the sheared DNA with the carrier glycogen. The pellet was washed with 70% ethanol and then centrifuged again at full speed. The DNA pellet was then left to air dry. 20ul of 10mM Tris.Cl was used to resuspend the DNA pellet. 1ul aliquot of this resuspended DNA is diluted to be quantified using the Quant-iTTM PicoGreen kit. (Invitrogen, Molecular Probes, Cat No. P7589) Sequencing library preparation is performed using the NEBNext Ultra DNA library prep kit for Illumina (NEB, E7370S).

Mapping and Normalization

100 bp reads were mapped using an in-house written bioinformatics pipeline. First, each read was quality trimmed. This algorithm uses a sliding window of 3 nucleotides. The sliding window first advances from the 5' end of the read, removing the most 5' nucleotide until the mean of the scores of the nucleotides in a window is greater than 30. The sliding window then advances from the 3' end and does the same operation. The quality trimmed reads were then filtered for reads greater than 25 nucleotides in length. The output of the trimming software is then fed into another program that detects and removes AdPCR primer sequences introduced during the DamID randomization procedure. This program looks for oligonucleotide sequences corresponding to any DamID primer or adapter sequences. Typically, any read that contains the adapter sequences dsAdR are concatemers of the adaptors and are filtered away. Any read that has an internal AdPCR primer sequence is split into different reads with the sequence prior to the primer as one read and the one after the primer as another. The output of this program is then used in a series of mapping and post processing steps. Mapping onto the mouse genome assembly, mm9, was done using Bowtie1 with default settings. Importantly, during the randomization procedure, we might end up with truncated AdPCR sequences at either 5' or 3' ends that cannot readily be detected from the previous filtering

programs. This results in a small portion of our, otherwise, mappable reads unused in the first Bowtie. The unmapped reads from the first Bowtie are then processed by removing 13 nucleotides from the 5'end. These reads are then fed into Bowtie1 for the second time. Unmapped reads in the 2nd Bowtie will then be used for 3' end processing and a final Bowtie. However, we wish to recover the original sequence of the unmapped reads (ie non-5' trimmed sequences). Hence, the unmapped reads from the second Bowtie were search for, in the unmapped reads of the first Bowtie. Once these sequences have been retrieved, the 3' ends were trimmed by 13 nucleotides and passed through Bowtie1 for the last time. All 3 mapped sam files for each sample were concatenated and intersected using Bedtools with an interval file representing the mm9 genome that has been pre-binned by GATCs. The occurrences of the number of reads mapped to each bin is tabulated and normalized by the length of the bin and the number of reads for that sample. This score is then further normalized to the score of the respective bins obtained for the Dam only control to yield the relative occupancy of the protein of interest in each bin. A $\log_2$ ratio was obtained for each bin and stored in a bed file for display purposes and downstream bioinformatics analyses. Quality filtered reads (process of quality filtering described in the section Mapping of NGS reads) were converted to FASTA format and input into the RepeatMasker program using the following command: RepeatMasker –species mouse input.fa

4.7.6 LADetector

DamID array signal intensity data were lifted over to mm9 using the Galaxy converter tool, and then, data from replicate arrays were averaged together (Giardine et al., 2005; Blankenberg et al., 2010; Goecks et al., 2010). DamID data were quantile normalized and smoothed using the preprocessCore R package (Bolstad, 2003) and then segmented via a modified circular binary segmentation using the DNAcopy R package (Seshan and Olshen, 2014), which is an algorithm for identifying copy number difference, which "tests for change-points using a maximal *t*-statistic with a permutation reference distribution to obtain the corresponding *P*-value" (Venkatraman and Olshen, 2007). A sliding window approach with a window size of 2 kb was used to combine neighboring segments, using in-house perl scripts. Code and accessory scripts provided in detail in Appendix A.2.

CHAPTER 5: FUNCTIONAL CHARACTERISTICS AND SIGNIFICANT FEATURES OF LADS

5.1 Introduction

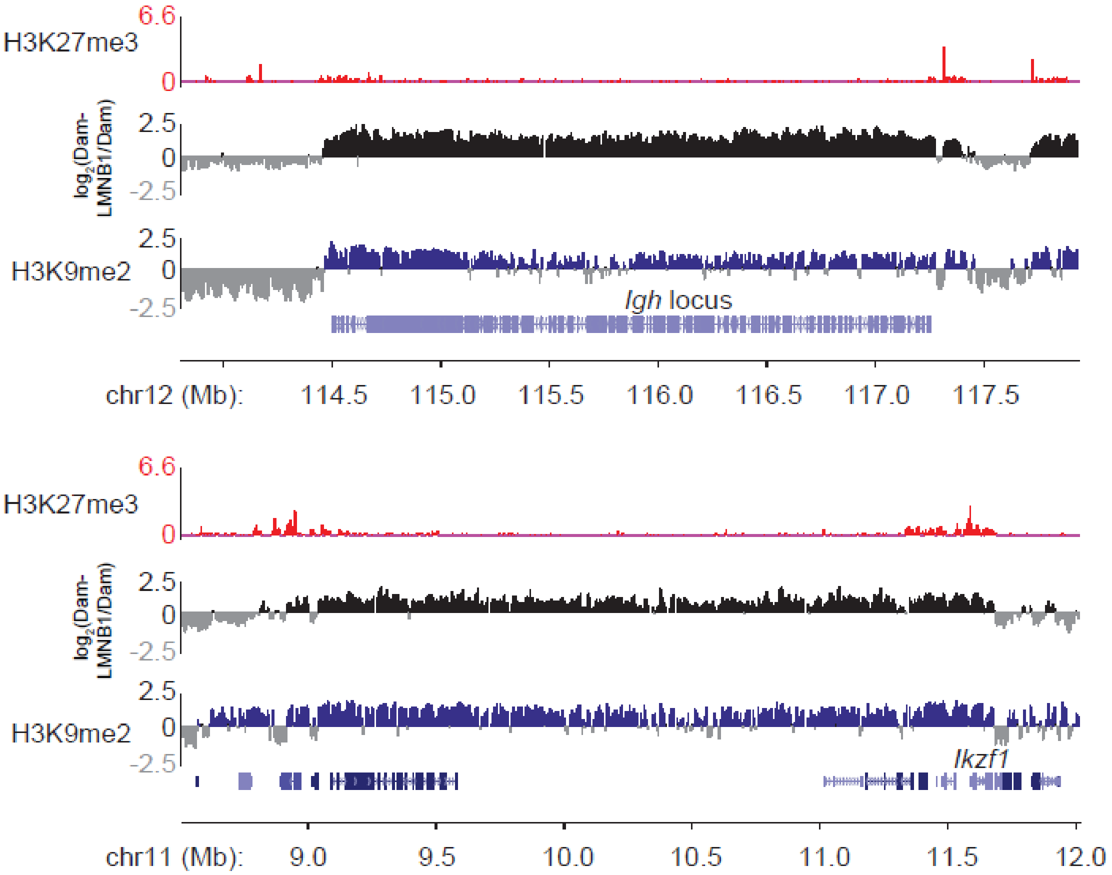
The development of more precise genomic coordinate definitions and a better understanding of the structure and function of the genome has allowed for closer observation of lamin associated domains. While we are beginning to understand the mechanisms behind LAD formation and maintenance, the genomic profile of LADs, outside of molecular association with the nuclear lamina, is still understudied. The observation that heterochromatin resides at the nuclear periphery has led to a number of hypotheses regarding the types of genomic features expected in LAD domains. The work presented here and in previous chapters aims to identify genome elements that may predict LAD presence or formation, or are features specific to LADs. Understanding the genomic and epigenomic features in the context of LADs will lend insight into structure, function, and mechanism of LAD formation and maintenance.

5.2 Heterochromatin features

As previously discussed, LADs are in contact with the nuclear periphery and are largely heterochromatic regions of the genome. Our studies of *de-novo* LAD formation indicate that histone H3K9me2/3 and H3K27me3 are important for normal LAD function. (Chapter 3 and Harr et al. 2015) Initial observations of LAD profiles across the genome did not indicate any specific heterochromatic marks; H3K9me2 was suggested but not shown to be correlated (Guelen et al. 2008). Histone H3K9me2 is a facultative heterchromatin mark associated with development, mainly deposited by G9a as a precursor to H3K9me3. A study published in 2009 focused on genome-wide profiles of H3K9me2 and discovered that there are large chromatin domains of this mark, and called them Large Organized Chromatin K9 modifications (LOCKs). (Wen et al. 2009) This study observed that H3K9me2 patterns over the genome have similar characteristics to, and cover approximately the same size regions as LADs. When those authors compared human placenta LOCKs to LADs from human lung fibroblasts, they found an 82% correlation, but in different cell types. In collaboration with those authors (the Feinberg group), we hypothesized that LADs and LOCKs cover the same genomic regions, and these elements may be important for establishment and/or maintenance of the other. I performed native ChIP in the same cell types where I collected LAD data through DamID (fibroblasts, pro-B cells, and pre-pro-B cells), and found that while LADs and LOCKs have high degree of overlap (~50%-80%, dependent on cell type), there are many regions where we find LADs and no LOCKS, and LOCKs and no LADs (Figure 35 and 36).

Figure 35 LADs and heterochromatin features

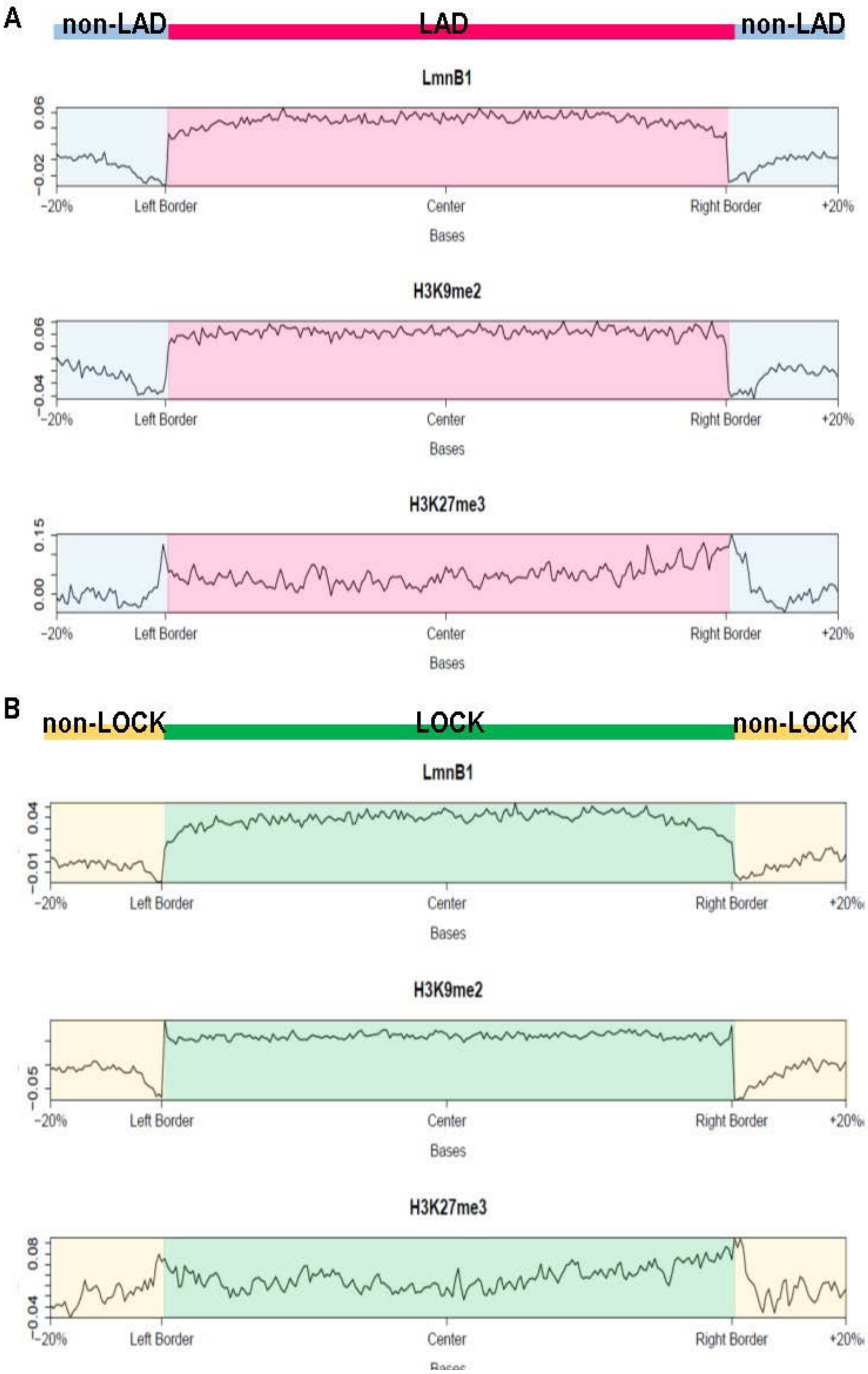
LADs (black), LOCKS (H3K9me2, blue) and H3K27me3 (red) align on the genome at specific loci. H3K27me3 is found at the borders of LADs and LOCKs, while LOCK domains show striking similarity to LADs.



From these experiments, we conclude that while LADs and LOCKs have a high degree of overlap and are linked, individually, each may serve distinct functions and the mechanisms driving the establishment/maintenance of each may not be the same. Since the initial description of LOCKs, the LOCK definition has expanded to include K3K9me2/3, and there are instances in the literature suggesting that H3K9me2/3 may be important for LAD formation, including our own data (Chapter 2, Chapter 3, Harr et al. 2015; Bian et al. 2013; Towbin et al. 2012).

Figure 36 Genome wide alignment of LADs and heterochromatin domains

(A) Genome-wide LADs aligned and plotted against LaminB1, H3K9me2 and H3K27me3 intensities demonstrate global patterns of geterochromatin. Pink shading denotes interior of the LAD, blue shading is outside of LADs. Line overplot indicates average signal intensity of listed feature (LaminB1, H3K9me2, H3K27me3) for all LADs. (B) LOCKs analyzed in the same way show patterning.



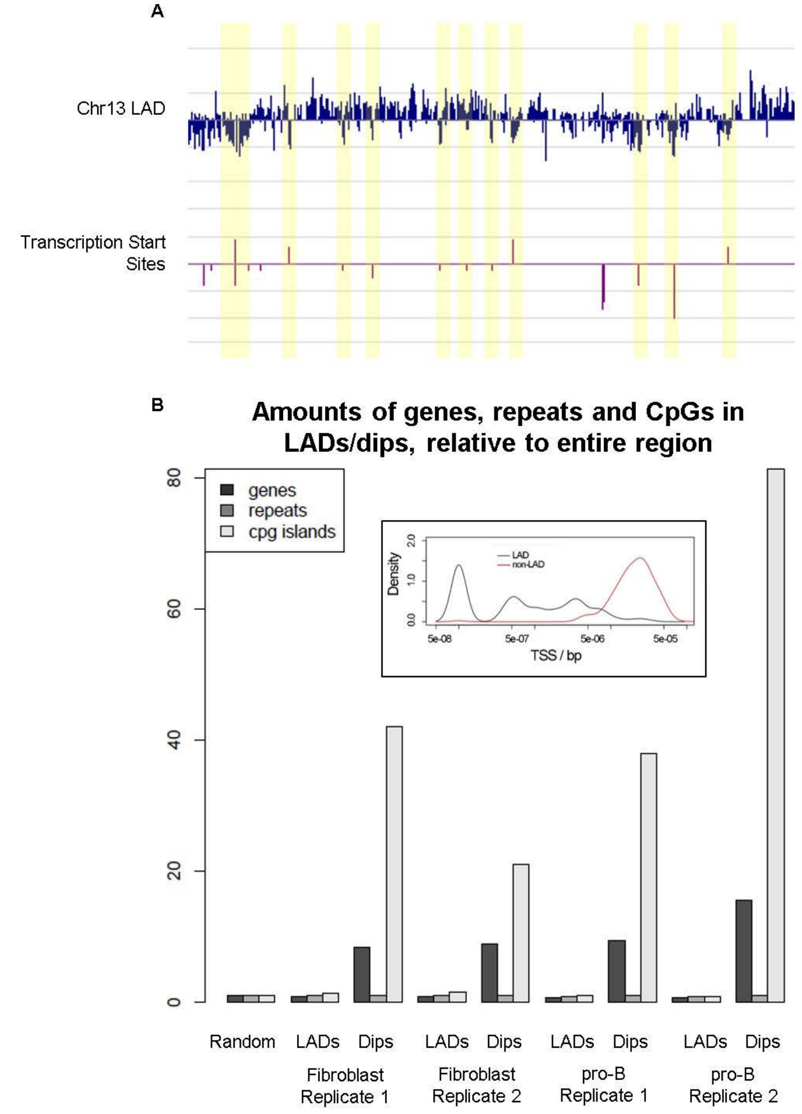
Given our previous epigenome perturbation data and recruitment studies, we favor a model that suggests H3K9me2/3 and H3K27me3 are both important for LAD function, stability and establishment.

5.3 Genic features

5.3.1 Dips

Figure 37 Dips within LADs

(A) Within LADs, there are often regions of lamina low or negative DamID signal that coincide with transcription start sites. (B) Genome wide in both fibroblasts and pro-B cells, CpGs, which correspond with transcription start sites, are highly enriched in Dips, although globally, transcription start sites are not enriched in LADs (B, inset)



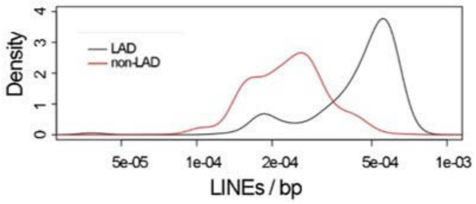
While defining the LADetector algorithm we noticed that some LADs were interrupted by small regions of non-LADs, or negative lamin association. We decided to define these regions as included within a larger LAD domain and define these regions as 'Dips (Figure 37)'. An examination of Dips defined by microarray DamID data shows that they are enriched in transcription start sites and CpGs in the genome. Another group also observed negative regions within LOCK domains, and termed them ‘euchromatin islands’ (Wen et al. 2012). We hypothesize that these regions are important for normal genome function and allow for dynamic gene activation, silencing, and ongoing-transcription within LAD domains.

5.3.2 LINE elements

Also during the initial evaluation of LADs and definition of LADs by the LADetector, it became apparent that LINE elements are enriched in LAD domains, especially in murine cell types (Figure 38). By observing LINE patterning, one could predict with some certainty the presence of a LAD. As LINEs are generally A/T rich, LADs are also enriched with A/T sequences.(Zullo et al. 2012)

Figure 38 LINEs are enriched in LADs

Density of LINEs per basepair is plotted for LAD and nonLADs.



5.4 Discussion

Early analysis of LAD domains provided little evidence of a specific chromatin signature that defined LADs. (Guelen et al. 2008) Investigation by us and others has revealed that the epigenome is linked to LADs, especially heterochromatin marks H3K9me2/3, or LOCKs, that reside throughout the body of LADs, and H3K27me3 which are enriched at the borders of LADs. Additional analyses of genomic features in the context of LADs have revealed a few characteristics that further suggest functionality and dynamics of the peripheral compartment. Consistent with gene-poor and repressed chromatin, LINE elements and A/T sequences are enriched in LADs. Promoters in adjacent domains drive transcription away from LAD border regions, perhaps contributing to the delineation of the borders (Guelen et al. 2008). It is interesting to note that H3K9me2/3 domains that correlate highly with LADs have “islands of euchromatin” within a larger LOCK domain, as evidenced by low H3K9me2/3 signal, and these islands overlap with transcription start sites and Dips (Wen et al. 2012). The potential functional role of these regions is unknown, but they may be indicative of regulatory regions important to LAD dynamics and/or may have a role in scaffolding (Schematic provided in Figure 39).

The heterochromatin patterning combined with the higher-order chromatin organization data (TADs) and our cytological data from previous chapters lead us to believe that LADs are a phenomenon of the 3D epigenome and cannot be strictly defined by the 2D genome. While there are definite trends in the 2D data, the most significant data regarding LADs come from 3D studies.

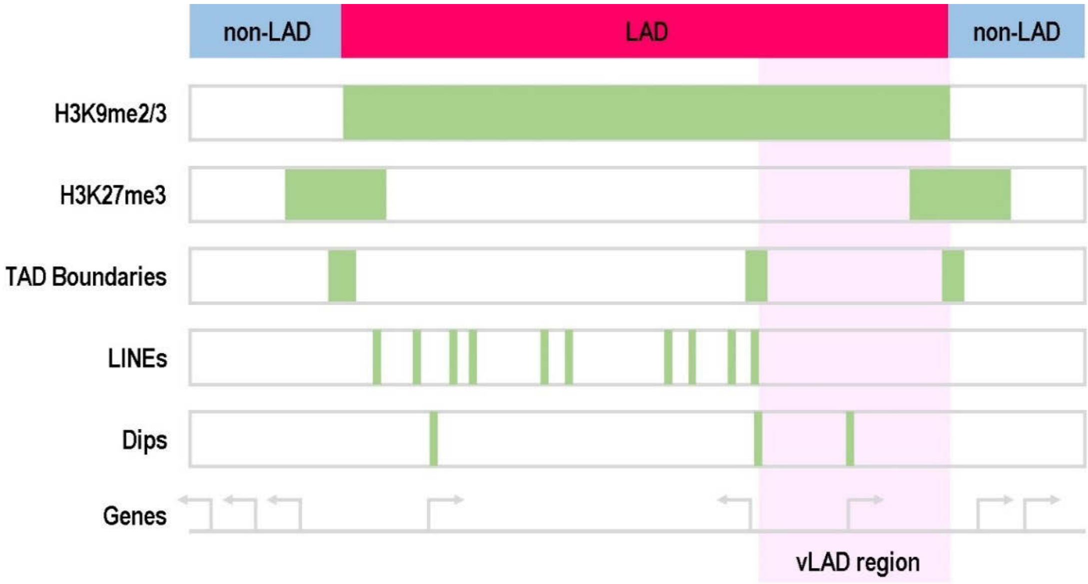


Figure 39 LAD features.

Features of LADs described through this work are aligned to show a basic identity of LAD domains based on 2D and 3D genomic data.

CHAPTER 6: DISCUSSION

Throughout this work we have studied how to better identify Lamin Associated Domains with increased accuracy and precision at defining border regions, as well as the functional implications of LAD organization. Our comprehensive LAD maps have allowed us to uncover aspects of the 3D genome such as epigenetic identity of LADs, genomic features contained within LADs, sequences that establish chromatin association with the nuclear periphery, and a novel and unique sub-chromosome architecture. We have also shown that in certain cell states, such as through development and in disease-like models, nuclear architecture is re-structured. Specifically we see this in in B-cell development (Chapter 3), epigenome instability (Chapter 4) and perturbation of nuclear integrity (Chapter 4). In chapter 2, I describe our work defining a precise algorithm to identify LADs, which has enabled us to study functional organization of the genome (Chapter 3), and the mechanisms that contribute to directed reorganization of the genome observed in development (Chapter 4).

The discovery that sub-chromosomal organization is ordered into domains relative to the nuclear periphery is an interesting and important result. Such functional organization had only been hinted at, and this work represents the first visualization of sub-chromosome domains. Additionally, this is the first study to use genome-wide, population-based, molecular data to visualize chromatin on a global level in single cells. The development and application of these novel FISH probes expands the tools available to the field for studying nuclear architecture, and also enables us to understand that the protein composition of the nuclear lamina plays an important role in maintaining proper organization. In addition, we were able to compare our LAD maps to other data examining higher-order structure, and found that LAD and chromosome organization falls in line with these topological domains, and is possibly modular, based on the boundaries of the TAD domains. By comparing the LAD profiles across multiple cell types and throughout a developmental program, we are able to better understand how specific reorganization of the genome accompanies the changes in transcription, morphology, and function that define cell states. Having an accurate map of LADs in different cell types allowed us to identify variable LADs and we discovered that these variable regions contain sequences, Lamin Associating Sequences, which direct to the nuclear periphery and may govern cell-type specific architecture.

All this data suggests that there exists a normal 3D genome architecture that is consistent with a healthy cell state. Therefore, it is possible that disruptions of the epigenome may lead to disease. While there are documented cases of diseases that also have known disruptions of the epigenome or proteins that govern nuclear integrity, it is unclear what the underlying mechanism for disease pathology is. Additionally, large disruptions (additions or subtractions) of the genome may demonstrate pathology related to underlying genome disorganization. Such diseases exist, such as progeria (resulting from a nuclear lamina protein gene mutation), Down Syndrome (Trisomy 21), and different cancer phenotypes where the epigenome is disrupted. The study of 3D architecture in these disease states will be critical to a full understanding to disease etiology and may also lead to discovery of target therapies. Also in the literature, there are a few examples of single genes also being redirected to the nuclear periphery that may be a pathogenic feature of the disease, such as the triplet-repeat disorder Friedreich's ataxia (FRDA). In FRDA, there is an expansion of a GAA.TTC triplet repeat in the Frataxin gene (FXN) gene that leads to patients with neurological damage and movement problems. Very recently it was shown that these expanded triplet-repeat expansions direct to the nuclear periphery and that tandem repeats direct to the nuclear periphery and likely form a *de novo* LAD, characterized by association with the nuclear periphery and an accumulation of H3K9me3 and H3K27me3 over the locus. Thus, the mechanism that leads to disease in FRDA patients may be related to genome organization and LAD establishment and formation. Further investigation is necessary to determine the extent that disease is precipitated by disruptions in nuclear architecture, and the tools and strategies presented here will certainly enable those studies.

In summary, this doctoral work presents the development of new technologies for studying genome organization. Through the establishment of new tools and technologies, the field has gained an understanding of functional sub-organization of chromosomes as an avenue to discovery that deepens our understanding of the genome. The identification and profiling of variable LADs and genome organization in differing cell types, such as the experiments presented in Chapters 3 and 4 examining B cell development, is necessary to initiate subsequent studies to better understand how genome organization may be involved in regulation of development and disease. Additionally, the understanding of how regions of chromatin direct to the nuclear periphery, how LADs are maintained in the peripheral zone, and what leads to chromosome disorganization during development and disease provides a target for study and potential therapy development.

APPENDICES

A.1 DamID experiments

Cell Type	**Experiment Type**	**Platform**	**Filename**	**Notes**
Fibroblast	DamID	Array	354882_3T3_LAD_1.tabular	NIH3T3
Fibroblast	DamID	Array	356132_3T3_LAD_2.tabular	NIH3T3
Fibroblast	DamID	Array	356401_3T3LAD_dyeswap.tabular	NIH3T3
Fibroblast	DamID	Array	356401_3T3LAD_dyeswap.tabular	NIH3T3
Fibroblast	ChIP H3K9me2	Array	356450_3T3_LOCK_expt2.tabular	NIH3T3
Fibroblast	ChIP H3K9me2	Array	356691_3T3_LOCK1.tabular	NIH3T3
Fibroblast	ChIP H3K9me2	Array	356692_3T3_LOCK_2.tabular	NIH3T3
Fibroblast	ChIP H3K9me2	Array	439582_3T3_LOCK_expt3.tabular	NIH3T3
MEF	ChIP H3K9me2	Array	439582R_B6WTMEF3_LOCK_expt4.tabular	Primary
MEF	DamID	Array	439583R_B6WTMEF3_LAD.tabular	Primary
pre-pro-B	DamID	Array	439586_EBF_LAD.tabular	EBF-/-
pre-pro-B	ChIP H3K9me2	Array	439623_EBF_LOCK_expt4.tabular	EBF-/-
pro-B	DamID	Array	439834_RPB2_LAD.tabular	Rag2-/-, Population 2, RPB2
pro-B	ChIP H3K9me2	Array	439832_RPB2_LOCK_expt4.tabular	Rag2-/-, Population 2, RPB2
pro-B	DamID	Array	356417_RPB3LAD_dyeswap.tabular	Rag2-/-, Population 3, RPB3
pro-B	DamID	Array	439880_RPB3_LAD_expt4.tabular	Rag2-/-, Population 3, RPB3
pro-B	DamID	Array	356685_RPB3_LAD1.tabular	Rag2-/-, Population 3, RPB3
pro-B	DamID	Array	356687_RPB3_LAD_2.tabular	Rag2-/-, Population 3, RPB3
pro-B	ChIP H3K9me2	Array	357627_RPB3_LOCK_2.tabular	Rag2-/-, Population 3, RPB3

pro-B	ChIP H3K9me2	Array	439583_RPB3_LOCK_expt3.tabular	Rag2-/-, Population 3, RPB3
pro-B	ChIP H3K9me2	Array	356556_RPB3_LOCK_expt2.tabular	Rag2-/-, Population 3, RPB3
pre-pro-B	DamID	Sequencing		EBF-/-
pre-pro-B	DamID	Sequencing		EBF-/-
pro-B	DamID	Sequencing		Rag2-/-, Population 3, RPB3
MEF	DamID	Sequencing		X17, Wildtype
MEF	DamID	Sequencing		X17, TSA treated
MEF	DamID	Sequencing		X17, DZNep treated
MEF	DamID	Sequencing		X17, Bix treated
MEF	DamID	Sequencing		X17, DMSO treated
MEF	DamID	Sequencing		1.8, Wildtype
MEF	DamID	Sequnecing		1.8, TSA treated
MEF	DamID	Sequencing		1.8, DZNep treated
MEF	DamID	Sequencing		1.8, Bix treated
MEF	DamID	Sequencing		1.8, DMSO treated

A.2 Definition of LADs and Dips – LADetector version 1

A.2.1 Information and directions for script use

To define LADs, we created and used a new algorithm, the LADetector, as published in *Directed targeting of chromatin to the nuclear lamina is mediated by chromatin state and A-type lamins.* Harr JC, **Luperchio TR**, Wong X, Cohen E, Wheelan SJ, Reddy KL. 2015 January 5 and available online. Code is reprinted in part here.

For use of scripts to define LADs -

Workflow:

1. rscript_normalization_segmentation_1.txt - R
2. segmentation_consolidate_chrnames_2.pl - perl
3. segmentation_refine_3.pl - perl

Experiment preparation:

Place all array data in a single directory.

Create a text file called "list_of_files.txt" with experiment file names in a list, and place this list in the same directory as your samples. All experiments listed will be quantile normalized together.

***This workflow requires all input data to be identical (ie comparing different samples hybridized from the same platform) and probes must be ordered identically in all files. Original sample data must be in the format of "chr, start, stop, value". If defining LAD regions from multiple data sets not on the same platform or with identical probe/map locations, normalize (if necessary) and segment separately (as done in section 2 of "rscript_normalization_segmentation_1.txt") and continue with the perl scripts.

rscript_normalization_segmentation_1.txt:

Using R, run "rscript_normalization_segmentation_1.txt". This script is divided into sections. Section 1 combines all the like samples in your directory into a table, with each column being a data set, and each row is a probe/map location. The table will be in the format of "chr, start, stop, sample1, sample2, ..." with headers. The samples are then quantile normalized and this normalized table of all samples is printed to your directory and is what is used in the next section.

Section 2 uses the package "DNAcopy" (Seshan VE and Olshen A. DNAcopy: DNA copy number data analysis. R package version 1.40.0.) to segment each sample from your quantile normalized array of data. This will take some time. At the end of processing, each individual segmented sample is printed to your working directory with .seq extension (column_name.seg).

segmentation_consolidate_chrnames_2.pl:

Each .seg file generated from the previous segmentation is to be run through perl script "segmentation_consolidate_chrnames_2.pl". This script is to consolidate the segmentation, and the result is a ".consolidated.txt" file in your directory.

segmentation_refine_3.pl:

Each file generated from "segmentation_consolidate_chrnames_2.pl" is to run through perl script "segmentation_refine_3.pl". This script defines LAD regions from the segmentation. It windows the genome over 2kb regions, and positive regions separated by small negative regions to be defined as one unit. LAD regions are returned as a .lad file. This file is in GFF format.

A.2.2 rscript_normalization_segmentation_1.txt – R

```
# This is a comment line
# Make a text file that has a list of all your filenames
# Put all your files in the same directory and set your working directory
library(DNAcopy)
library(preprocessCore)
# This first part makes a table with all your data, with column names as your original file names
tab <- read.table("file1.tabular", header=TRUE, row.names=NULL) #this is one of your experimental files, you need this for your genome coordinates
tab <- tab[,1:3]
list_of_files <- read.table("list_of_files.txt")
head(list_of_files)
for (i in 1:length(list_of_files[,1]))
{ myfile = list_of_files[i,]
myfile <- as.character(myfile)
tmpfile <- read.table(myfile, header=TRUE, row.names=NULL)
tab <- cbind(tab, tmpfile[,4])
names <- c(names, myfile)
}
subtab <- tab[,4:length(tab[1,])]
subtab <- normalize.quantiles(as.matrix(subtab)) # Quantile normalization
tab <- cbind(tab[,1:3], subtab)
# Check the names of tab
# You may need
        #names2 <- names[2:length(names)]
        #names3 <- c("chr", "start", "stop", names2)
names(tab) <- names # or names(tab) <- names3
write.table(tab, "all_files_normalized.txt", row.names=FALSE, col.names=TRUE, quote=FALSE) # This makes a new file in your directory

# This next part is the segmentation
complete_tab <- tab # unncessary, for cosmetics if running at the same time as above. If running separately, read in your normalized file here.
samples <- names(complete_tab)
for (i in 4:length(samples))
{
  copynum <- CNA(complete_tab[,i], complete_tab[,1], complete_tab[,2], data.type="logratio");
  smooth_cn <- smooth.CNA(copynum)
  ssc <- segment(smooth_cn, alpha=0.001)
  filename=paste(samples[i], ".seg", sep="");
```

```
  write(t(ssc$output), sep="\t", ncolumns=6, file=filename)
}
```

You should have as many files as samples in your directory. Run these through the perl scripts.

A.2.3 segmentation_consolidate_chrnames_2.pl – perl

```
#!/usr/bin/perl
open (FILE, "$ARGV[0]");
open (OUT, ">$ARGV[0].consolidated.txt");
$line = <FILE>;
$line =~ s/\n//;
@array = split(/\t/, $line);
$lastchr = $array[1];
$laststart = $array[2];
$laststop = $array[3];
$lastnum = $array[5];
while ($line = <FILE>){
  $line =~ s/\n//;
  @array = split(/\t/, $line);
  if (samesign($lastnum, $array[5]) && $array[1] eq $lastchr)
  {
    $laststop = $array[3];
  } else
  {
    if (samesign($lastnum, 1)){
      $lastnum = 1;
    } else {
      $lastnum = -1;
    }
    print OUT ("$ARGV[0]\t$lastchr\t$laststart\t$laststop\t10\t$lastnum\n");
    $lastchr = $array[1];
    $laststart = $array[2];
    $laststop = $array[3];
    $lastnum = $array[5];
  }
}
if (samesign($lastnum, 1)){
  $lastnum = 1;
} else {
  $lastnum = -1;
}
print OUT ("$ARGV[0]\t$lastchr\t$laststart\t$laststop\t10\t$lastnum\n");
```

```
sub samesign
{
  my ($first, $last) = @_;
  if (abs($first + $last) == abs($first) + abs($last)){
    return 1;
  } else
  {
    return 0;
  }
}
```

A.2.4 segmentation_refine_3.pl - perl

```
#!/usr/bin/perl

$filename = $ARGV[0];
if ($filename eq "")
{
  die ("need consolidated seg file");
}
$filelist[0] = $filename;
$window = 2000;
$maxdipsize = 7000;
for ($i=0; $i<(@filelist-0); $i++)
{
  @ladstart = ();
  @ladstop = ();
  @ladchr = ();
  @dipstart = ();
  @dipstop = ();
  @dipchr = ();
  open (FILE, "$filelist[$i]");
  $tmpname = $filelist[$i];
  $tmpname =~ s/\.txt//;
  while ($line = <FILE>)
  {
    @array = split(/\s+/, $line);
    if ($array[1] == $lastchr)
    {
      if ($array[5] =~ /-/)  ##potential dip
      {
        if ($array[3] - $array[2] <= $maxdipsize && $lastlad - $array[2] <= $window)
##size of dip & spacing from lad
```

```
        {
          $possdipchr = $array[1];
          $possdipstart = $array[2];
          $possdipstop = $array[3];
        }
      } else
      {
        if ((@ladstop-0)>0 && $possdipstop > 0 && $array[2] - $possdipstop <=
$window) ##last was a dip, add and merge lads
        {
          $dipchr[(@dipchr-0)] = $possdipchr;
          $dipstart[(@dipstart-0)] = $possdipstart;
          $dipstop[(@dipstop-0)] = $possdipstop;
          $ladstop[(@ladstop-1)] = $array[3];
        } else
        {
          $ladchr[(@ladchr-0)] = $array[1];
          $ladstart[(@ladstart-0)] = $array[2];
          $ladstop[(@ladstop-0)] = $array[3];
        }
        $lastlad = $ladstop;
        $possdipchr = $possdipstart = $possdipstop = 0;
      }
    } else  #starting a new chromosome, don't have to check last entry
    {
      if ($array[5] =~ /-/)  ##potential dip
      {
        $possdipchr = $array[1];
        $possdipstart = $array[2];
        $possdipstop = $array[3];
      } else
      {
        $ladchr[(@ladchr-0)] = $array[1];
        $ladstart[(@ladstart-0)] = $array[2];
        $ladstop[(@ladstop-0)] = $array[3];
      }
    }
    $lastchr = $array[1];
  }
  $filename = $filelist[$i];
  $filename = $filename . ".lads";
  open (OUT, ">$filename");
```

```
  for ($j=0; $j<(@ladchr-0); $j++)
  {
    if ($ladstop[$j] > $ladstart[$j])
    {
      print                                                                                   OUT
("$ladchr[$j]\t$filename\t$filename\t$ladstart[$j]\t$ladstop[$j]\t+\t.\n");
    }
  }
}
```

A.3 Fluorescence in-situ hybridization using coverslips for high-resolution microscopy

Modified and adapted from previously published 3D-immunoFISH protocol, Reddy 2008

Prepare coverslips and cells

Coat 18x18 glass coverslips with 0.5-1mg/mL poly-L-lysine. Submerge coverslips or float on a drop of solution for 10 minutes. You must use 18x18 coverslips that are optimal for viewing with your objectives. Allow the coverslip to dry, then rinse with sterile water. Place coverslip in appropriate dish and UV sterilize coverslip if culturing cells overnight. Plate cells and allow to grow for desired time and confluence.

Day 1 FISH

Solutions are standard for FISH as described in protocol for slides and conditions are empirically determined per cell line. Conditions indicated here are for primary fibroblasts

Fix coverslips by aspirating media and flooding with 4% paraformaldehyde/1xPBS solution for 15 minutes, then washing 3 times, 5 minutes each time, with PBS. Incubate coverslips with 0.5% saponin,0.5% TritonX-100 in 1xPBS for 15 minutes, wash again, 3 times, 5 minutes each. Treat coverslips with 0.1N HCl for 12 minutes, then incubate for 1 hour at room temperature or 4 degrees overnight in 20% glycerol in 1xPBS. After incubation, freeze thaw coverslips 3-4 times in liquid nitrogen using FINE TIPPED forceps. It is important that you use extremely fine forceps or you risk damaging your samples and cracking the coverslips. When freezing, you must wait a few seconds before attempting to remove the coverslips from the forceps or you will rip the cells from the surface. Use the freeze-thawed coverslips immediately or store at -80.

Hybridization

Carefully handling the coverslips with fine forceps at all steps, thaw coverslips at room temperature and wash 3 times with 1xPBS. Watch the coverslips carefully that they do not dry out, the edges will become dry very quickly. Treat coverslips with 100ug/mL RNAse for 30minutes-1hour in 2x SSC at room temperature in a humidified chamber. Hybridize coverslips by washing in 70% formamide at 76'C for 3 minutes, then 50% formamide at 76'C for 1 minute in small coplin jars designed for coverslips. Drain coverslip quickly with a kimwipe, and then hybridize with probe/hybridization solution (probe, 9ug salmon sperm DNA, 6ug placental DNA, 3ug Cot-1 DNA, 50% dextran sulfate, 50% formamide) by sealing the coverslip onto a glass slide with rubber cement and then incubating 16-36 hours at 37'C in a humidified chamber.

Develop

Carefully and slowly peel rubber cement away from coverslips and incubate slides+coverslips in 2xSSC until the coverslips fall off. Retrieve coverslip and wash them 3 times, 7 minutes each wash in 50% formamide/2xSSC at 47'C and subsequently wash coverlsips 3 times with 63'C .2xSSC. Mount and seal coverslips if no further labeling is needed. For immunofluorescence, block with 4% BSA in 1x PBS for 30 minutes, then incubate with primary antibody in same blocking medium 1 hour room temperature or overnight at 4'C. Wash coverslips briefly 3 times with 1xPBS/.05%TX-100, and then incubate with secondary antibody in blocking medium for 1 hour at room temperature. Post incubation, wash slides 3 times, 5 minutes per wash with 1x PBS .05%TX100. Counterstain DNA as needed. Mount and seal coverslips for viewing and imaging.

A.4 Variable LADs during pre-pro-B to pro-B transition

vLADs in pre-proB to proB Transition

Chr	pre-proB vLAD start	pre-proB vLAD stop	RefSeq Gene Name	RefSeq Common Gene Name
1	6904562	7546653	NM_183028	Pcmtd1
1	9398291	9460954		
1	10380660	10517030	NM_001289497	Cpa6
1	10380660	10517030	NM_177834	Cpa6
1	14901186	15629345	NM_177781	Trpa1
1	14901186	15629345	NM_001098528	Kcnb2
1	16828894	17129868	NM_020604	Jph1
1	21999937	22704268	NM_183018	Rims1
1	21999937	22704268	NM_053270	Rims1
1	21999937	22704268	NM_001012623	Rims1
1	21999937	22704268	NM_001012625	Rims1
1	21999937	22704268	NM_001012624	Rims1
1	23744915	23745551		
1	24505697	24508247	NM_007733	Col19a1
1	30809204	30826792		
1	31270017	31291169	NR_033445	4931428L18Rik
1	31270017	31291169	NM_029062	Pih1d3
1	31909226	32286966	NM_133235	Khdrbs2
1	32620992	33502128	NM_133235	Khdrbs2
1	42500208	42560490		
1	44481225	44938649	NM_028450	Gulp1
1	44481225	44938649	NR_040602	4930521E06Rik
1	46760963	46812997	NM_001310335	Dnah7c
1	46979629	47303129		
1	50890679	50935842		
1	57122530	57124409		
1	71026625	71269330	NM_007525	Bard1
1	71529987	71530166		
1	89926706	89928485		
1	95736007	95737846	NM_178882	D2hgdh
1	95736007	95737846	NM_001310767	D2hgdh
1	96088259	97660206	NR_040473	4930440C22Rik
1	96088259	97660206	NM_026321	Fam174a
1	96088259	97660206	NM_009183	St8sia4
1	96088259	97660206	NM_001159745	St8sia4
1	96088259	97660206	NR_040479	4930598F16Rik
1	98653283	98798885	NM_172658	Slco4c1
1	98653283	98798885	NR_131964	Panct2
1	98881940	98939959	NR_120500	Slco6b1
1	99425608	99443933		
1	99495256	99495698		
1	101438138	102855719	NM_172851	Cntnap5b
1	108918391	108930198		
1	109230702	109407456	NM_025867	Serpinb11
1	109230702	109407456	NM_027548	Serpinb7
1	122935206	122937012		

Chr	proB vLAD start	proB vLAD stop	RefSeq Gene Name	RefSeq Common Gene Name
1	4252961	4328703	NM_001195662	Rp1
1	5315316	5416942		
1	6094994	6121229		
1	12667604	12835382	NM_001198566	Sulf1
1	12667604	12835382	NM_001198565	Sulf1
1	12667604	12835382	NM_172294	Sulf1
1	20428191	20444433	NM_153179	Pkhd1
1	23193016	23456858	NR_029533	Mir30a
1	23193016	23456858	NR_029717	Mir30c-2
1	23193016	23456858	NM_001081079	Ogfrl1
1	24329078	24678750	NM_007733	Col19a1
1	24824409	24843844		
1	31374784	31419971		
1	40494623	41261363	NM_001294171	Il1rl1
1	40494623	41261363	NM_001025602	Il1rl1
1	40494623	41261363	NM_010743	Il1rl1
1	40494623	41261363	NM_001161842	Il18r1
1	40494623	41261363	NM_001161843	Il18r1
1	40494623	41261363	NM_008365	Il18r1
1	40494623	41261363	NM_010553	Il18rap
1	40494623	41261363	NM_177084	Slc9a4
1	40494623	41261363	NM_001033289	Slc9a2
1	40494623	41261363	NM_172499	Mfsd9
1	40494623	41261363	NM_001081198	Tmem182
1	40494623	41261363	NR_040475	4930448I06Rik
1	43031030	43031996	NM_053107	Gpr45
1	44263695	44297266	NM_207281	Mettl21e
1	45323127	45765467	NM_009930	Col3a1
1	45323127	45765467	NM_007737	Col5a2
1	45979749	46063711	NM_016917	Slc40a1
1	51094792	51097853	NM_019790	Tmeff2
1	56032625	56042604		
1	56814692	56882744	NM_139146	Satb2
1	61110431	63038703	NR_040483	9530026F06Rik
1	61110431	63038703	NM_001081050	Pard3b
1	61110431	63038703	NM_010939	Nrp2
1	61110431	63038703	NM_001077403	Nrp2
1	61110431	63038703	NM_001077406	Nrp2
1	61110431	63038703	NM_001077405	Nrp2
1	61110431	63038703	NM_001077404	Nrp2
1	61110431	63038703	NM_001077407	Nrp2
1	61110431	63038703	NR_040601	4930487H11Rik
1	63249684	64086093	NM_146250	Gpr1
1	63249684	64086093	NM_001285937	Zdbf2
1	63249684	64086093	NM_001285936	Zdbf2
1	63249684	64086093	NM_028673	Zdbf2

1	123103376	123105657		
1	130813121	132309619	NM_172485	Thsd7b
1	130813121	132309619	NM_001317361	Cd55b
1	130813121	132309619	NM_007827	Cd55b
1	132391845	132392807		
1	141415185	141428449	NM_031164	F13b
1	144610387	145394573		
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9	80789515	82678342	NM_175213	Mei4
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9	83829221	84384975	NM_199195	Bckdhb
9	85211154	85261737	NM_001160378	Fam46a
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9	85522695	85718556	NM_001081282	Ibtk
9	86204929	86435035	NM_027394	Ube2cbp
9	86204929	86435035	NM_177208	Dopey1
9	87152808	87345937		
9	89477960	89684808	NM_153509	AF529169
9	89477960	89684808	NM_025360	Tmed3
9	89477960	89684808	NM_207260	Ankrd34c
9	91247899	91311421	NM_009573	Zic1
9	91247899	91311421	NM_009576	Zic4
9	91996487	92533424	NM_001195693	Plscr5
9	91996487	92533424	NM_011636	Plscr1
9	91996487	92533424	NR_105808	Mir6386
9	91996487	92533424	NM_001195084	Plscr2
9	91996487	92533424	NM_008880	Plscr2
9	91996487	92533424	NM_001033184	1700057G04Rik
9	91996487	92533424	NM_178711	Plscr4
9	91996487	92533424	NR_029474	B430319G15Rik
9	91996487	92533424	NM_011961	Plod2
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9	94397169	95425319	NM_001033145	1190002N15Rik
9	94397169	95425319	NM_177909	Slc9a9
9	94397169	95425319	NR_106116	Mir7656
9	94397169	95425319	NM_018763	Chst2
9	94397169	95425319	NM_001114977	U2surp
9	94397169	95425319	NM_026476	U2surp
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9	98140250	98156521		
9	98734045	98822315	NM_001134660	Prr23a1
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9	98734045	98822315	NM_028033	Prr23a3
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9	104504904	105245586	NM_028719	Cpne4
9	104504904	105245586	NM_053159	Mrpl3
9	104504904	105245586	NM_029385	Nudt16
9	104504904	105245586	NM_028562	1700080E11Rik
9	104504904	105245586	NM_172461	Nek11
9	109051064	109663779	NM_177069	Fbxw21
9	109051064	109663779	NM_177598	Fbxw13
9	109051064	109663779	NM_001008428	Fbxw20
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9	109051064	109663779	NM_015793	Fbxw14
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9	109051064	109663779	NM_001013776	Fbxw24
9	109051064	109663779	NM_001033794	Fbxw18
9	109051064	109663779	NM_198674	Fbxw26
9	111457534	111487838	NM_016853	Stac
9	111767624	112526493	NM_001177618	Arpp21
9	111767624	112526493	NM_001177616	Arpp21
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9	111767624	112526493	NM_001177617	Arpp21
9	111767624	112526493	NR_029823	Mir128-2
9	111767624	112526493	NM_001177619	Arpp21
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X	7904265	10106798	NM_199064	Ssxb10
X	7904265	10106798	NM_199066	Ssxb9
X	7904265	10106798	NM_026492	Ssxb1
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X	7904265	10106798	NM_001001450	Ssxb2
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X	7904265	10106798	NM_198898	Ssxb3
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X	7904265	10106798	NM_001085524	Fthl17b
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X	7904265	10106798	NM_001277184	Fthl17-ps1
X	7904265	10106798	NM_001099326	Fthl17d
X	7904265	10106798	NM_031261	Fthl17e
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X	7904265	10106798	NM_001038697	Fthl17f
X	7904265	10106798	NM_001270700	4930402K13Rik
X	7904265	10106798	NM_173414	Lancl3
X	7904265	10106798	NM_023500	Xk
X	7904265	10106798	NM_029588	1700012L04Rik

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X	7904265	10106798	NM_007807	Cybb
X	7904265	10106798	NM_001085517	Gm5132
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X	7904265	10106798	NM_026096	Hypm
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X	13721109	18050748	NM_001034100	Gm5382
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X	13721109	18050748	NM_025738	Cypt1
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X	13721109	18050748	NM_172778	Maob
X	13721109	18050748	NM_010883	Ndp
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X	13721109	18050748	NM_001313746	Fundc1
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X	13721109	18050748	NR_132634	4930578C19Rik
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X	46008148	47063947	NM_001271451	Enox2
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X	56312473	57771325	NM_001290415	Fgf13
X	56312473	57771325	NM_010200	Fgf13
X	56312473	57771325	NR_030574	Mir504
X	56312473	57771325	NM_007979	F9
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X	56312473	57771325	NM_001289730	Mcf2
X	56312473	57771325	NM_001289731	Mcf2
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X	100228230	100461889	NM_008671	Nap1l2
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X	101815613	102957192	NM_175358	Zdhhc15
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X	101815613	102957192	NM_053206	Magee2
X	101815613	102957192	NR_015467	5530601H04Rik
X	101815613	102957192	NM_001281871	Pbdc1
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X	101815613	102957192	NM_053201	Magee1
X	101815613	102957192	NR_002167	E530001F21Rik
X	101815613	102957192	NR_029910	Mir384
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X	103436241	105030948	NM_001033424	Fnd3c2
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X	110009546	110081418		
X	110344801	111211716	NM_001289734	Dach2
X	110344801	111211716	NM_001289733	Dach2
X	110344801	111211716	NM_001289732	Dach2
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X	140904245	142923810	NM_178358	Lhfpl1
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X	155346479	155358577		
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X	160912839	161306843	NM_027027	Asb9
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X	165159857	165311818	NM_009707	Arhgap6
X	166065496	166094407		
Y	806784	1973345	NM_009571	Zfy2
Y	806784	1973345	NM_001113395	Gm16501
Y	806784	1973345	NM_001177569	Gm6026
Y	806784	1973345	NM_011564	Sry

A.5 Variable LADs after TSA treatment

vLADs in TSA (Compared to DMSO)									
Gained					Lost				
Chr	LAD Start	LAD Stop	RefSeq Gene Name	Ref Seq Common Gene Name	Chr	LAD Start	LAD Stop	RefSeq Gene Name	Ref Seq Common Gene Name
1	9801497	9921483	NM_177547	Sgk3	1	5070685	5143308	NM_133826	Atp6v1h
1	9801497	9921483	NM_133220	Sgk3	1	5070685	5143308	NM_001310442	Atp6v1h
1	9801497	9921483	NM_001037759	Sgk3	1	6400368	6461255		
1	9801497	9921483	NM_177722	Mcmdc2	1	15265674	15438279	NM_001098528	Kcnb2
1	10291459	10442760	NM_001289497	Cpa6	1	87627721	87683660	NM_177055	A630001G21Rik
1	10291459	10442760	NM_177834	Cpa6	1	87627721	87683660	NR_106172	Mir8096
1	10763785	10925019			1	87627721	87683660	NR_108086	9930111H07Rik
1	10951901	11487964	NM_029525	Prex2	1	101172346	101258849		
1	10951901	11487964	NM_001033636	Prex2	1	134422509	134503763	NM_177129	Cntn2
1	10951901	11487964	NM_001160371	A830018L16Rik	1	134422509	134503763	NM_001160318	Nfasc
1	10951901	11487964	NM_177173	A830018L16Rik	1	134422509	134503763	NM_001160317	Nfasc
1	10951901	11487964	NM_001160369	A830018L16Rik	1	134422509	134503763	NM_182716	Nfasc
1	10951901	11487964	NM_001160370	A830018L16Rik	1	134422509	134503763	NM_001160316	Nfasc
1	10951901	11487964	NM_001310451	A830018L16Rik	1	138638112	138712422		
1	11772038	12550676	NM_177173	A830018L16Rik	1	143843349	143908956		
1	11772038	12550676	NM_001160369	A830018L16Rik	1	193915984	193994444	NM_011633	Traf5
1	11772038	12550676	NM_001310451	A830018L16Rik	1	193915984	193994444	NM_144814	Rcor3
1	11772038	12550676	NR_105759	Mir6341	1	193915984	193994444	NM_001290282	Rcor3
1	12803181	12871444	NM_001198566	Sulf1	1	193915984	193994444	NM_001290278	Rcor3
1	12803181	12871444	NM_001198565	Sulf1	1	193915984	193994444	NM_001290279	Rcor3
1	12803181	12871444	NM_172294	Sulf1	1	193915984	193994444	NM_001290280	Rcor3
1	12803181	12871444	NM_172841	Slco5a1	1	193915984	193994444	NR_033536	Gm10516
1	13367858	13549244			2	49170796	49300624	NM_029924	Mbd5
1	13748781	13910701	NR_004447	Gm5523	2	49170796	49300624	NM_001290656	Mbd5
1	13921299	14055483			2	106190352	106261224		
1	15791819	15907467	NM_001286628	Terf1	2	112965048	113042926	NM_001319156	Ryr3
1	15791819	15907467	NM_009352	Terf1	2	147386325	147465203		
1	15791819	15907467	NM_001033288	Sbspon	2	181029026	181093977	NM_009133	Stmn3
1	16106056	16167981	NM_133832	Rdh10	2	181029026	181093977	NM_001001882	Rtel1
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X	148837673	149090102	NM_172441	Shroom2
X	149208222	149276487	NM_010951	Gpr143
X	149792680	149856412	NM_173780	Klf8
X	150082764	150164214	NM_175429	Kctd12b
X	150082764	150164214	NM_027327	2210013O21Rik
X	151518144	151685810	NM_020015	Magea1
X	151518144	151685810	NM_001081671	Cldn34b2
X	151518144	151685810	NM_009121	Sat1
X	151518144	151685810	NM_001291865	Sat1
X	151777750	151859865		
X	152084506	153887697	NR_033598	4930503H13Rik
X	152084506	153887697	NM_011077	Phex
X	152084506	153887697	NM_009214	Sms
X	154054103	154125531		
X	155350217	155685673		
X	155827930	156054338	NM_001313751	Map7d2
X	155827930	156054338	NM_001081124	Map7d2
X	155827930	156054338	NM_001313752	Map7d2
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X	155827930	156054338	NM_001033472	A830080D01Rik
X	156436303	156544302	NM_001163085	Map3k15
X	156611207	156926125	NM_001290445	Adgrg2
X	156611207	156926125	NM_001079848	Adgrg2
X	156611207	156926125	NM_178712	Adgrg2
X	156611207	156926125	NM_001079847	Adgrg2
X	156611207	156926125	NM_001290446	Adgrg2
X	156611207	156926125	NM_001079857	Adgrg2
X	156961947	157477898	NM_001177879	Phka2
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X	156961947	157477898	NM_172783	Phka2
X	156961947	157477898	NM_011147	Ppef1
X	156961947	157477898	NM_011302	Rs1
X	156961947	157477898	NM_001024624	Cdkl5
X	156961947	157477898	NM_001001496	Gja6
X	158259247	158341822	NM_001290526	Nhs
X	158259247	158341822	NM_001081052	Nhs
X	159590901	160301664	NM_008177	Grpr
X	159590901	160301664	NM_028842	Rnf138rt1
X	160412991	160590529	NM_181315	Car5b
X	160412991	160590529	NM_001308386	Siah1b
X	160412991	160590529	NM_009173	Siah1b
X	160412991	160590529	NM_001308385	Siah1b
X	160412991	160590529	NM_020626	Tmem27
X	160412991	160590529	NM_001313719	Tmem27
X	160412991	160590529	NM_001130513	Ace2
X	160412991	160590529	NM_027286	Ace2
X	161331204	161403347	NM_001290524	Mospd2
X	161331204	161403347	NM_001290523	Mospd2
X	161331204	161403347	NM_029730	Mospd2
X	164128254	165071186	NM_001290427	Frmpd4
X	164128254	165071186	NM_001033330	Frmpd4
X	164128254	165071186	NM_001290428	Frmpd4
X	165236276	165315083	NM_009707	Arhgap6
X	166426821	166649596	NM_001290512	Mid1
X	166426821	166649596	NM_010797	Mid1
X	166426821	166649596	NM_001290504	Mid1
X	166426821	166649596	NM_001290506	Mid1
X	166426821	166649596	NM_001290505	Mid1
Y	0	2687244	NM_009570	Zfy1
Y	0	2687244	NM_011667	Uba1y
Y	0	2687244	NM_011419	Kdm5d
Y	0	2687244	NM_012011	Eif2s3y
Y	0	2687244	NR_027507	Tspy-ps
Y	0	2687244	NM_009484	Uty
Y	0	2687244	NM_012008	Ddx3y
Y	0	2687244	NM_148943	Usp9y
Y	0	2687244	NM_009571	Zfy2
Y	0	2687244	NM_001113395	Gm16501
Y	0	2687244	NM_001177569	Gm6026
Y	0	2687244	NM_011564	Sry
Y	0	2687244	NM_001113395	Gm16501
Y	0	2687244	NM_001177569	Gm6026
Y	0	2687244	NM_001166384	Rbmy
Y	0	2687244	NM_001270515	Gm21704
Y	0	2687244	NM_001270516	Gm21708
Y	0	2687244	NM_001270518	Gm4064
Y	0	2687244	NM_011253	Rbmy
Y	0	2687244	NM_001270511	Gm10352
Y	0	2687244	NM_001270513	Gm21677
Y	0	2687244	NM_001270514	Gm21693
Y	0	2687244	NM_001270510	Gm10256
Y	0	2687244	NM_001166384	Rbmy
Y	0	2687244	NM_001270514	Gm21693
Y	0	2687244	NM_001270515	Gm21704
Y	0	2687244	NM_001270516	Gm21708
Y	0	2687244	NM_011253	Rbmy
Y	0	2687244	NM_001270513	Gm21677
Y	0	2687244	NM_001270512	Gm3376

A.6 Variable LADs after BIX01294 treatment

vLADs in BIX01294 Treatment (Compared to DMSO)									
Gained					Lost				
Chr	LAD Start	LAD Stop	RefSeq Gene Name	Ref Seq Common Gene Name	Chr	LAD Start	LAD Stop	RefSeq Gene Name	Ref Seq Common Gene Name
1	12476935	12550676			1	4751800	4841581	NM_025300	Mrpl15
1	40613944	40683417	NM_177084	Slc9a4	1	4751800	4841581	NM_001177658	Mrpl15
1	43638065	43725743			1	4751800	4841581	NR_033530	Mrpl15
1	77676547	77876659			1	4751800	4841581	NM_008866	Lypla1
1	121708688	121815734	NM_019933	Ptpn4	1	10442760	10531078	NM_001289497	Cpa6
1	121708688	121815734	NM_175106	Tmem177	1	10442760	10531078	NM_177834	Cpa6
1	122043326	122120540	NM_028439	3110009E18Rik	1	13101655	13172054	NM_001081209	Prdm14
1	122043326	122120540	NM_001172074	3110009E18Rik	1	13101655	13172054	NM_008678	Ncoa2
1	123332516	123393170	NM_001025156	Ccdc93	1	13101655	13172054	NM_001302702	Ncoa2
1	123332516	123393170	NM_029955	Ccdc93	1	13549244	13658063	NM_028173	Tram1
1	146251014	146324854			1	13549244	13658063	NM_145381	Lactb2
1	159115048	159209484	NM_177644	Rasal2	1	14151017	14249132	NM_010164	Eya1
1	160787801	160896360	NM_001085376	Pappa2	1	14151017	14249132	NM_001252192	Eya1
1	165652299	165742822	NM_001143956	Mettl11b	1	14151017	14249132	NM_001310459	Eya1
1	165652299	165742822	NM_010629	Kifap3	1	14310196	14403377		
1	165652299	165742822	NM_001305643	Kifap3	1	15265674	15438279	NM_001098528	Kcnb2
1	179563307	179631087	NR_037994	2310043L19Rik	1	17595795	17651668	NM_053191	Pi15
1	185506434	185724651			1	21431351	21959957	NM_001310477	Kcnq5
1	190912249	190986447			1	21431351	21959957	NM_001160139	Kcnq5
1	191059226	191248129	NM_001281848	Kcnk2	1	21431351	21959957	NM_023872	Kcnq5
1	191059226	191248129	NM_010607	Kcnk2	1	24552620	24820147	NM_007733	Col19a1
1	191059226	191248129	NM_001159850	Kcnk2	1	24552620	24820147	NM_026719	Lmbrd1
1	191059226	191248129	NM_001281847	Kcnk2	1	24552620	24820147	NM_001310483	Lmbrd1
2	8538382	8592449			1	42209319	42280858		
2	48173262	48234342			1	44636068	44790555	NM_028450	Gulp1
2	48387079	48653472			1	45223187	45345149		
2	57033205	57086304	NR_040356	BB557941	1	47372230	47429441		
2	57033205	57086304	NR_040633	4930555B11Rik	1	51405410	51506156		
2	65121077	65192196	NM_177074	Slc38a11	1	53918898	54064218	NM_001001883	Hecw2
2	79694839	79785246	NM_016744	Pde1a	1	53918898	54064218	NM_172655	Hecw2
2	79694839	79785246	NM_001159582	Pde1a	1	54097553	54260636	NM_001001883	Hecw2
2	79694839	79785246	NM_001009978	Pde1a	1	54097553	54260636	NM_172655	Hecw2
2	79694839	79785246	NM_001009979	Pde1a	1	60689037	60791426		
2	80048988	80133240	NM_177256	Prdx6b	1	61795577	61932869	NM_001081050	Pard3b
2	90249502	90301269	NM_001135657	Ptprj	1	61942282	62044798	NM_001081050	Pard3b
2	90249502	90301269	NM_008982	Ptprj	1	63264844	63344250	NM_001285937	Zdbf2
2	102436052	102507334	NM_173749	Pamr1	1	63264844	63344250	NM_001285936	Zdbf2
2	102436052	102507334	NM_001077514	Slc1a2	1	63264844	63344250	NM_028673	Zdbf2
2	108669394	108776733			1	63264844	63344250	NM_001267872	Zdbf2
2	109057750	109150299	NM_029790	Mettl15	1	63486730	64131366	NM_011780	Adam23
2	109057750	109150299	NM_139303	Kif18a	1	63486730	64131366	NM_001081658	Dytn
2	127878003	127930100	NM_028765	Acoxl	1	63486730	64131366	NM_029696	Mdh1b
2	134263808	134342435	NM_010403	Hao1	1	63486730	64131366	NM_172422	Fastkd2
2	139938990	140006506	NM_001081090	Esf1	1	63486730	64131366	NM_001256158	4933402D24Rik
2	139938990	140006506	NM_027093	Ndufaf5	1	63486730	64131366	NR_027824	Gm13749
2	143839191	143926207	NM_001044750	Banf2	1	63486730	64131366	NM_033563	Klf7
2	143839191	143926207	NM_207275	Banf2	1	63486730	64131366	NR_105864	Mir6899
2	160605296	160664326	NM_177263	Zhx3	1	64174308	64565804		
2	160716730	160866260	NM_022883	Lpin3	1	69567311	69737719	NM_011770	Ikzf2
2	160716730	160866260	NM_001199118	Lpin3	1	70115811	70333535	NM_029160	Spag16
2	160716730	160866260	NM_001291145	Emilin3	1	70115811	70333535	NM_025728	Spag16
2	160716730	160866260	NM_182840	Emilin3	1	70882375	71164976	NM_177164	Vwc2l
2	160716730	160866260	NR_126509	Chd6	1	70882375	71164976	NM_001310658	Vwc2l
2	160716730	160866260	NM_173368	Chd6	1	70882375	71164976	NM_007525	Bard1
3	20616683	20740570			1	72614862	72669933	NM_018817	Smarcal1
3	39500905	39557618			1	76127516	76308054		
3	57475470	57534498	NM_001033349	Ankub1	1	76825866	76998077		
3	58406648	58479580	NM_001081262	Erich6	1	77008964	77324751		
3	58406648	58479580	NR_004433	Gm8234	1	78735812	78801095		
3	58406648	58479580	NM_009174	Siah2	1	78942115	79246919		
3	76434726	76519794	NM_178673	Fstl5	1	80703737	80864455	NM_175291	Dock10
3	76434726	76519794	NM_001253719	Fstl5	1	81280041	81375273		
3	80574910	80705677	NM_013540	Gria2	1	82488180	82780469	NM_007735	Col4a4
3	80574910	80705677	NM_001083806	Gria2	1	82488180	82780469	NM_007734	Col4a3
3	80574910	80705677	NM_001039195	Gria2	1	82488180	82780469	NM_001310699	Mff
3	80574910	80705677	NM_010298	Glrb	1	82488180	82780469	NM_029409	Mff
3	80574910	80705677	NM_001281969	Glrb	1	82488180	82780469	NM_001310695	Mff
3	86364920	86582158	NM_030695	Lrba	1	82488180	82780469	NM_001310697	Mff
3	86364920	86582158	NM_001077688	Lrba	1	82488180	82780469	NM_025453	Tm4sf20
3	86364920	86582158	NM_001077687	Lrba	1	83704607	84498155	NM_001003948	Pid1
3	99878053	99963724	NM_028892	Spag17	1	83704607	84498155	NR_105771	Mir6353
3	99878053	99963724	NM_175552	Wdr3	1	83704607	84498155	NM_152915	Dner
3	126844176	127122690	NR_105029	LOC100862268	1	84520858	84579548	NM_152915	Dner
3	126844176	127122690	NR_105030	LOC100862268	1	87627721	87688943	NM_177055	A630001G21Rik
3	130438522	130557606			1	87627721	87688943	NR_106172	Mir8096
3	130666427	130753786			1	87627721	87688943	NR_108086	9930111H07Rik
3	134985505	135051384	NM_178877	Slc9b2	1	88654418	89049497	NM_153530	Dis3l2
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3	137810252	137876412	NM_175389	Trmt10a	1	88654418	89049497	NM_007433	Alppl2
3	137810252	137876412	NM_001163386	4930579F01Rik	1	88654418	89049497	NM_001081082	Alpi
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3	137810252	137876412	NR_045760	0610031O16Rik	1	88654418	89049497	NM_001277925	Ecel1
3	141120661	141201945	NM_001293561	Unc5c	1	88654418	89049497	NM_021306	Ecel1
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3	144581013	144703524	NM_001033199	Clca4b	1	89313010	89402654	NM_001110212	Gigyf2
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3	157700491	157756739	NM_024194	Lrrc40	1	89313010	89402654	NM_019867	Ngef
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4	36521650	36573929	NM_001165999	Lingo2	1	115456753	115540965		
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4	43881347	43933734	NM_016678	Reck	1	122751467	123013775	NR_110450	Celrr
4	44256890	44324700	NM_010790	Melk	1	133583663	133801724	NM_145509	Rab7b
4	61005182	61055701	NM_008647	Mup2	1	133583663	133801724	NM_001311096	Rab7b
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4	105248444	105301079			1	133583663	133801724	NM_144875	Rab29
4	117497123	117564539	NM_008135	Slc6a9	1	134402357	134503763	NM_029025	Tmem81
4	117497123	117564539	NM_001034876	Ccdc24	1	134402357	134503763	NM_177129	Cntn2
4	117497123	117564539	NM_001253381	B4galt2	1	134402357	134503763	NM_001160318	Nfasc
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4	155412093	155562143	NR_132444	Gm13648
4	155412093	155562143	NR_029958	Mir429
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5	16166205	16265605		
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5	28360215	28421025	NM_153526	Insig1
5	54169161	54308909	NM_144517	Tbc1d19
5	58612637	58688462		
5	67659050	67720914	NM_028975	Tmem33
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5	67659050	67720914	NM_030108	Tmem33
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5	72972976	73030533	NM_007723	Cnga1
5	80913720	80994864		
5	82427348	82539406		
5	89309138	89389091	NM_001136260	Slc4a4
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5	119638644	119733917	NR_046033	Gm7538
5	147476898	147568153	NM_011669	Usp12
5	152181985	152232730	NR_045699	1700028E10Rik
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5	152181985	152232730	NR_131166	Gm3704
6	7350540	7451420		
6	7605617	7742955	NM_012055	Asns
6	77069447	77152803	NM_145732	Ctnna2
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6	77216523	77278336	NM_145732	Ctnna2
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6	83548034	83620478	NM_016751	Clec4f
6	91684749	91738592	NM_009320	Slc6a6
6	91684749	91738592	NM_001159507	Grip2
6	101509459	101569936		
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6	109842343	109905753		
6	112640445	112721171	NM_001167730	Rad18
6	112640445	112721171	NM_021385	Rad18
6	112640445	112721171	NM_080448	Srgap3
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1	139430474	139776811		
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1	139920975	140220460	NM_001268286	Ptprc
1	139920975	140220460	NM_177397	Atp6v1g3
1	140322842	140375185		
1	140575671	140640953	NR_040304	Gm5833
1	140815834	141108872	NM_001166501	Dennd1b
1	140815834	141108872	NM_181347	Dennd1b
1	140815834	141108872	NR_108103	4930596I21Rik
1	140815834	141108872	NM_133239	Crb1
1	143843349	143908956		
1	152402219	152481908	NM_001024720	Hmcn1
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2	68978110	69213590	NM_181547	Nostrin
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X	132660138	132869876	NM_001168578	Tceal8
X	132660138	132869876	NR_105804	Mir6383
X	132660138	132869876	NM_177919	Tceal5
X	132660138	132869876	NM_009052	Bex1
X	132660138	132869876	NM_001127169	Tceal7
X	132660138	132869876	NM_011712	Wbp5
X	132660138	132869876	NM_009750	Ngfrap1
X	132660138	132869876	NM_001110234	Ngfrap1
X	132660138	132869876	NM_001110233	Ngfrap1
X	133236069	133301407	NM_146236	Tceal1
X	133236069	133301407	NM_001168227	Morf4l2
X	133236069	133301407	NM_001168226	Morf4l2
X	133236069	133301407	NM_001168225	Morf4l2
X	133236069	133301407	NM_019768	Morf4l2
X	133236069	133301407	NM_001168228	Morf4l2
X	133236069	133301407	NM_001168230	Morf4l2
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X	133236069	133301407	NR_033324	BC065397
X	133236069	133301407	NM_010297	Glra4
X	133548726	133733862	NM_001082412	Slc25a53
X	133548726	133733862	NM_146261	Fam199x
X	133548726	133733862	NM_007957	Esx1
X	135720300	136098504	NM_001164630	Mum1l1
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X	135720300	136098504	NM_001164633	Mum1l1
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X	135720300	136098504	NM_175326	D330045A20Rik
X	135720300	136098504	NM_001254761	Rnf128
X	136355290	136553984	NM_029413	Morc4
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X	136355290	136553984	NM_001172148	Rbm41
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X	137984067	138175070	NM_007736	Col4a5
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X	137984067	138175070	NM_010572	Irs4
X	138454929	138730510	NM_001007576	Gucy2f
X	138454929	138730510	NM_001290532	Nxt2
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X	139711196	140262643	NM_001114385	Chrdl1
X	139711196	140262643	NM_031258	Chrdl1

X	139711196	140262643	NM_001195048	Pak3
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X	139711196	140262643	NM_001195049	Pak3
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X	139711196	140262643	NM_007603	Capn6
X	143754505	144054966	NM_008356	Il13ra2
X	143754505	144054966	NM_001306059	Il13ra2
X	143754505	144054966	NM_001081173	Lrch2
X	147915172	148077764	NM_001113354	Phf8
X	147915172	148077764	NM_177201	Phf8
X	149856412	149949304	NM_018798	Ubqln2
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X	152002002	152084506	NM_001093750	Ptchd1
X	153887697	154054103	NM_009214	Sms
X	153887697	154054103	NR_040420	Gm6568
X	153887697	154054103	NM_172307	Mbtps2
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X	155685673	155827930	NM_148945	Rps6ka3
X	155685673	155827930	NM_025437	Eif1ax
X	158341822	159590901	NM_001290526	Nhs
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X	158341822	159590901	NM_001290633	Reps2
X	158341822	159590901	NM_178256	Reps2
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X	158341822	159590901	NM_001168568	Ctps2
X	158341822	159590901	NM_001168569	Ctps2
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X	160590529	160900280	NM_001130513	Ace2
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X	160590529	160900280	NM_009759	Bmx
X	160590529	160900280	NM_027153	Pir
X	160590529	160900280	NM_001301402	Pir
X	160590529	160900280	NM_001308489	Figf
X	160590529	160900280	NM_010216	Figf
X	160590529	160900280	NM_011081	Piga
X	160590529	160900280	NM_001313737	Asb11
X	160590529	160900280	NM_026853	Asb11
X	165071186	165236276	NM_010832	Msl3
X	165071186	165236276	NM_009707	Arhgap6
X	165315083	166107188	NM_009707	Arhgap6
X	165315083	166107188	NM_178754	Arhgap6
X	165315083	166107188	NR_109847	Arhgap6
X	165315083	166107188	NM_001287530	Arhgap6
X	165315083	166107188	NM_001081978	Amelx
X	165315083	166107188	NM_001290371	Amelx
X	165315083	166107188	NM_009666	Amelx
X	165315083	166107188	NM_008222	Hccs

A.7 Variable LADs after DZNep treatment

vLADs in DZNep (Compared to DMSO)									
Gained					Lost				
Chr	LAD Start	LAD Stop	RefSeq Gene Name	Ref Seq Common Gene Name	Chr	LAD Start	LAD Stop	RefSeq Gene Name	Ref Seq Common Gene Name
1	9801497	9921483	NM_177547	Sgk3	1	6398290	6461255		
1	9801497	9921483	NM_133220	Sgk3	1	10442760	10544437	NM_001289497	Cpa6
1	9801497	9921483	NM_001037759	Sgk3	1	10442760	10544437	NM_177834	Cpa6
1	9801497	9921483	NM_177722	Mcmdc2	1	13549244	13658063	NM_028173	Tram1
1	16106056	16167981	NM_133832	Rdh10	1	13549244	13658063	NM_145381	Lactb2
1	39226712	39301164	NR_105767	Mir6349	1	14151017	14257115	NM_010164	Eya1
1	39226712	39301164	NM_008719	Npas2	1	14151017	14257115	NM_001252192	Eya1
1	51675406	51790387			1	14151017	14257115	NM_001310459	Eya1
1	54449162	54503799	NM_001033194	Gtf3c3	1	14305575	14403377		
1	55753609	55825984	NM_001114663	Plcl1	1	15327095	15438279	NM_001098528	Kcnb2
1	80643417	80703737	NM_175291	Dock10	1	17568764	17651668	NM_053191	Pi15
1	80643417	80703737	NM_001285927	Dock10	1	21431351	21959957	NM_001310477	Kcnq5
1	90152121	90241504	NM_001281466	Mroh2a	1	21431351	21959957	NM_001160139	Kcnq5
1	90152121	90241504	NM_198652	Hjurp	1	21431351	21959957	NM_023872	Kcnq5
1	90152121	90241504	NR_040291	6430706D22Rik	1	23831095	24127818	NM_172124	B3gat2
1	90152121	90241504	NM_172505	A730008H23Rik	1	23831095	24127818	NR_110972	Smap1
1	90152121	90241504	NM_134252	Trpm8	1	23831095	24127818	NM_028534	Smap1
1	123332516	123388921	NM_001025156	Ccdc93	1	23831095	24127818	NM_001290683	Smap1
1	123332516	123388921	NM_029955	Ccdc93	1	23831095	24127818	NM_026503	Sdhaf4
1	130175940	130240652	NM_026390	Ubxn4	1	23831095	24127818	NM_026604	Fam135a
1	130175940	130240652	NM_001081078	Lct	1	24552620	24820147	NM_007733	Col19a1
1	130175940	130240652	NM_008567	Mcm6	1	24552620	24820147	NM_026719	Lmbrd1
1	130175940	130240652	NM_001313695	Mcm6	1	24552620	24820147	NM_001310483	Lmbrd1
1	159119378	159209484	NM_177644	Rasal2	1	28037713	28124272		
1	162034514	162107214	NM_177839	Tnn	1	33540613	33715403	NM_008922	Prim2
1	190912249	190986447			1	34428588	34527982	NR_039562	Mir5103
1	191383015	191504482	NM_001081363	Cenpf	1	34428588	34527982	NM_027159	Ccdc115
2	5684700	5738567	NM_133837	Cdc123	1	34428588	34527982	NM_178601	Imp4
2	13955760	14008416	NM_001012396	Hacd1	1	34428588	34527982	NM_011206	Ptpn18
2	13955760	14008416	NM_013935	Hacd1	1	42209319	42288720		
2	13955760	14008416	NR_038162	Stamos	1	43323827	43449708		
2	13955760	14008416	NM_011484	Stam	1	47331803	47575670	NR_105768	Mir6350
2	16541279	16676325	NM_026162	Plxdc2	1	51364299	51513232	NR_045151	9330175M20Rik
2	57033205	57086304	NR_040356	BB557941	1	54011405	54064218	NM_001001883	Hecw2
2	57033205	57086304	NR_040633	4930555B11Rik	1	54011405	54064218	NM_172655	Hecw2
2	106564370	106634271	NM_001143683	Mpped2	1	54097553	54260636	NM_001001883	Hecw2
2	106564370	106634271	NM_029837	Mpped2	1	54097553	54260636	NM_172655	Hecw2
2	127612425	127750400	NM_016902	Nphp1	1	54655230	54838405	NM_001081433	Ankrd44
2	127612425	127750400	NM_001291013	Nphp1	1	59067311	59213768	NM_175200	Als2cr11
2	127612425	127750400	NM_001291012	Nphp1	1	59067311	59213768	NM_001033449	Tmem237
2	127612425	127750400	NR_015476	1500011K16Rik	1	59067311	59213768	NM_001037812	Tmem237
2	127612425	127750400	NM_009772	Bub1	1	59067311	59213768	NM_001164682	Mpp4
2	127612425	127750400	NM_001113179	Bub1	1	59067311	59213768	NM_145143	Mpp4
2	127612425	127750400	NM_028765	Acoxl	1	61795577	61932869	NM_001081050	Pard3b
2	139849206	139910039	NR_110350	Tasp1	1	61942282	62044798	NM_001081050	Pard3b
2	139849206	139910039	NM_001159640	Tasp1	1	62886355	62964659		
2	139849206	139910039	NM_001159641	Tasp1	1	63039535	63091477		
2	139849206	139910039	NM_175225	Tasp1	1	63654337	64133483	NM_001081658	Dytn
2	139849206	139910039	NR_110352	Tasp1	1	63654337	64133483	NM_029696	Mdh1b
2	139849206	139910039	NR_110351	Tasp1	1	63654337	64133483	NM_172422	Fastkd2
2	139849206	139910039	NM_001289611	Tasp1	1	63654337	64133483	NM_001256158	4933402D24Rik
2	139938990	139999020	NM_001081090	Esf1	1	63654337	64133483	NR_027824	Gm13749
2	139938990	139999020	NM_027093	Ndufaf5	1	63654337	64133483	NM_033563	Klf7
2	158632304	158697032	NM_001291144	Dhx35	1	63654337	64133483	NR_105864	Mir6899
2	158632304	158697032	NM_145742	Dhx35	1	64170203	64233685		
2	160605296	160664326	NM_177263	Zhx3	1	64278341	64552913		
2	160716730	160866260	NM_022883	Lpin3	1	65005308	65221280	NM_027582	Akr1cl
2	160716730	160866260	NM_001199118	Lpin3	1	65005308	65221280	NM_001310617	Akr1cl
2	160716730	160866260	NM_001291145	Emilin3	1	65005308	65221280	NM_007777	Cryge
2	160716730	160866260	NM_182840	Emilin3	1	65005308	65221280	NM_007776	Crygd
2	160716730	160866260	NR_126509	Chd6	1	65005308	65221280	NM_001082573	Crygc
2	160716730	160866260	NM_173368	Chd6	1	65005308	65221280	NM_007775	Crygc
2	173830917	173888062			1	65005308	65221280	NM_144761	Crygb
2	179494558	179567136	NM_001316723	Cdh4	1	65005308	65221280	NM_007774	Cryga
2	179494558	179567136	NM_009867	Cdh4	1	65005308	65221280	NM_001285882	D630023F18Rik
3	35769523	35848937	NM_033623	Dcun1d1	1	65005308	65221280	NM_175293	D630023F18Rik
3	35769523	35848937	NM_001205362	Dcun1d1	1	65005308	65221280	NM_001285881	D630023F18Rik
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3	126844176	126977442	NR_105029	LOC100862268	1	70115811	70333535	NM_029160	Spag16
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3	137996535	138063934	NR_033581	Adh6-ps1	1	70882375	71141378	NM_177164	Vwc2l
3	141117352	141198736	NM_001293561	Unc5c	1	70882375	71141378	NM_001310658	Vwc2l
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3	142162328	142231128	NM_153564	Gbp5	1	72614862	72669933	NM_018817	Smarcal1
3	142162328	142231128	NM_001083312	Gbp7	1	72805861	73533139	NM_008342	Igfbp2
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4	11954316	12009818	NM_177861	Tmem67	1	78818002	79246919		
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5	48590110	48710065	NR_111900	Slit2
5	48590110	48710065	NR_029798	Mir218-1
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1	83704607	84579548	NR_105771	Mir6353
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1	88131708	88234479	NM_030184	Armc9
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1	89319000	89402654	NM_146112	Gigyf2
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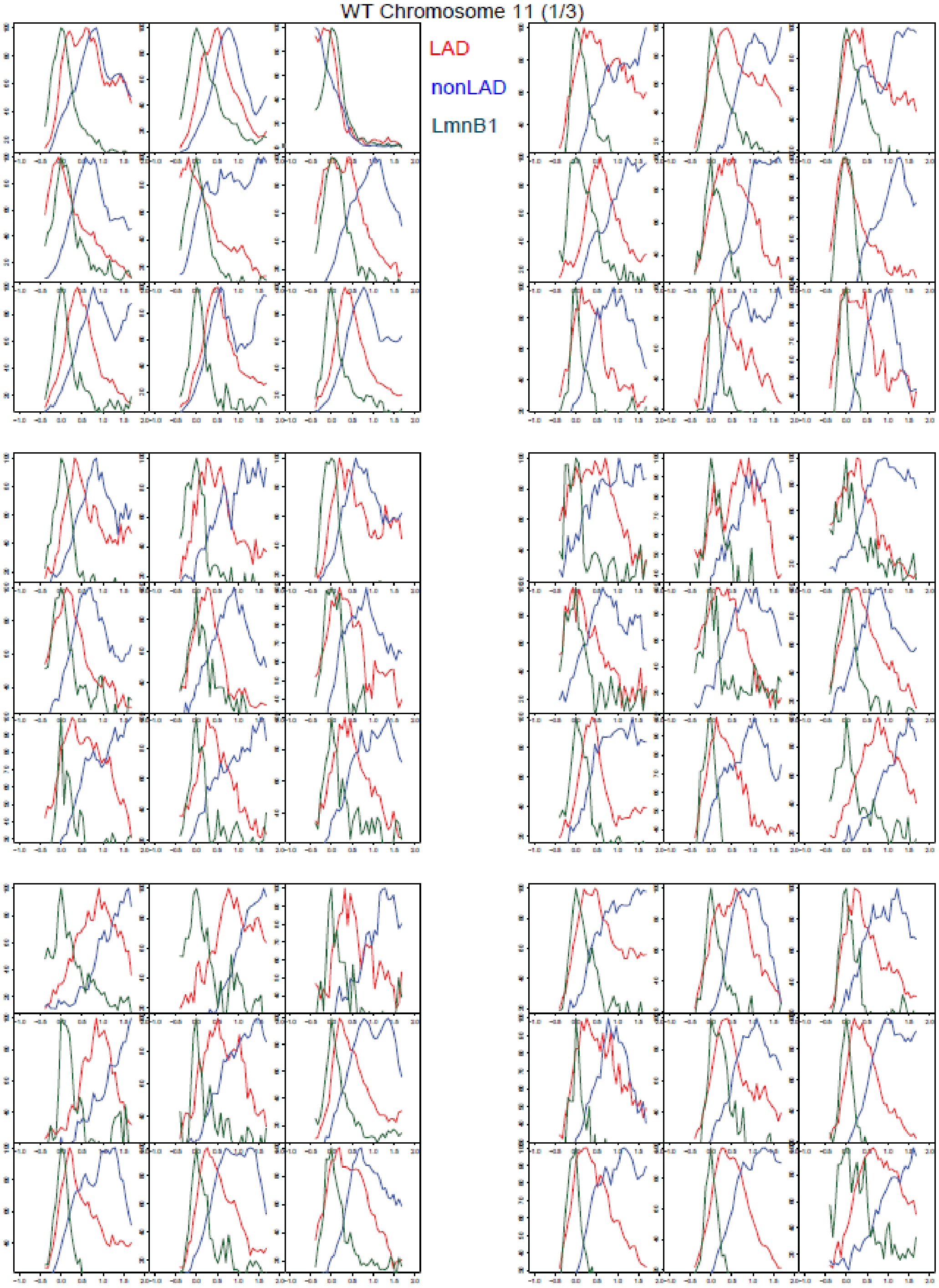
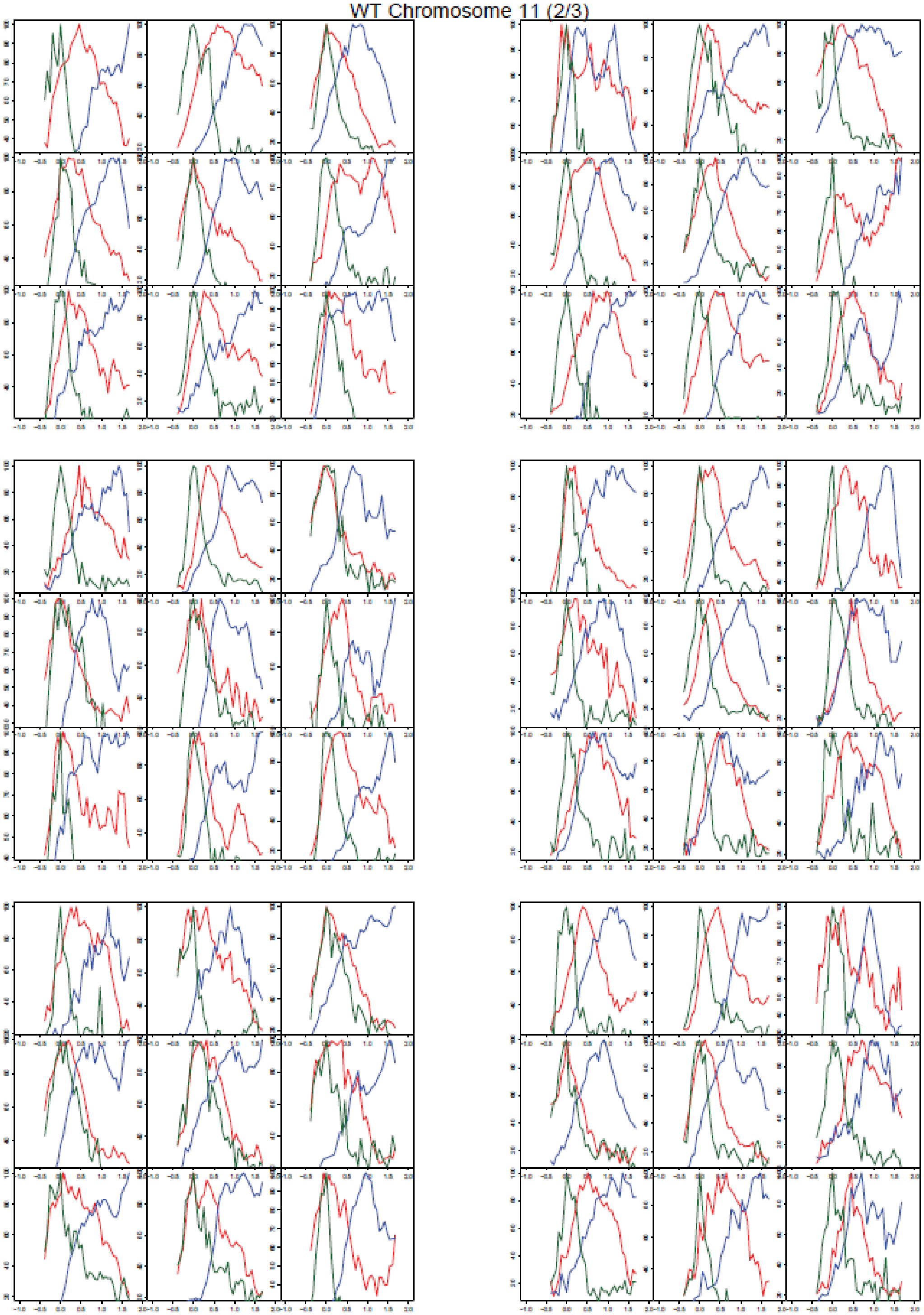
A.8 Individual Measurements for Wildtype Chromosomes 11 and 12

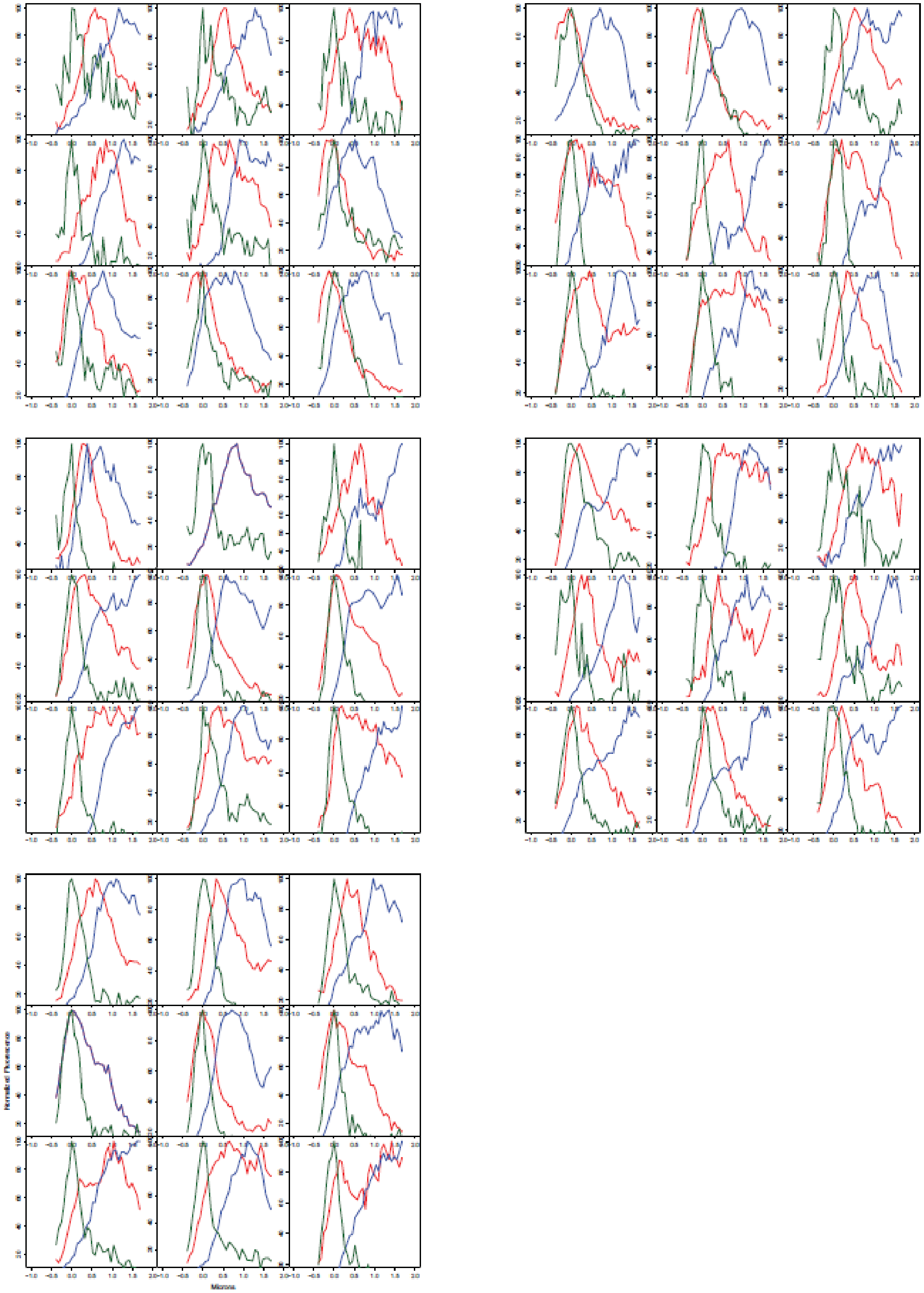
A.8.1 Chromosome 11 100x objective magnification



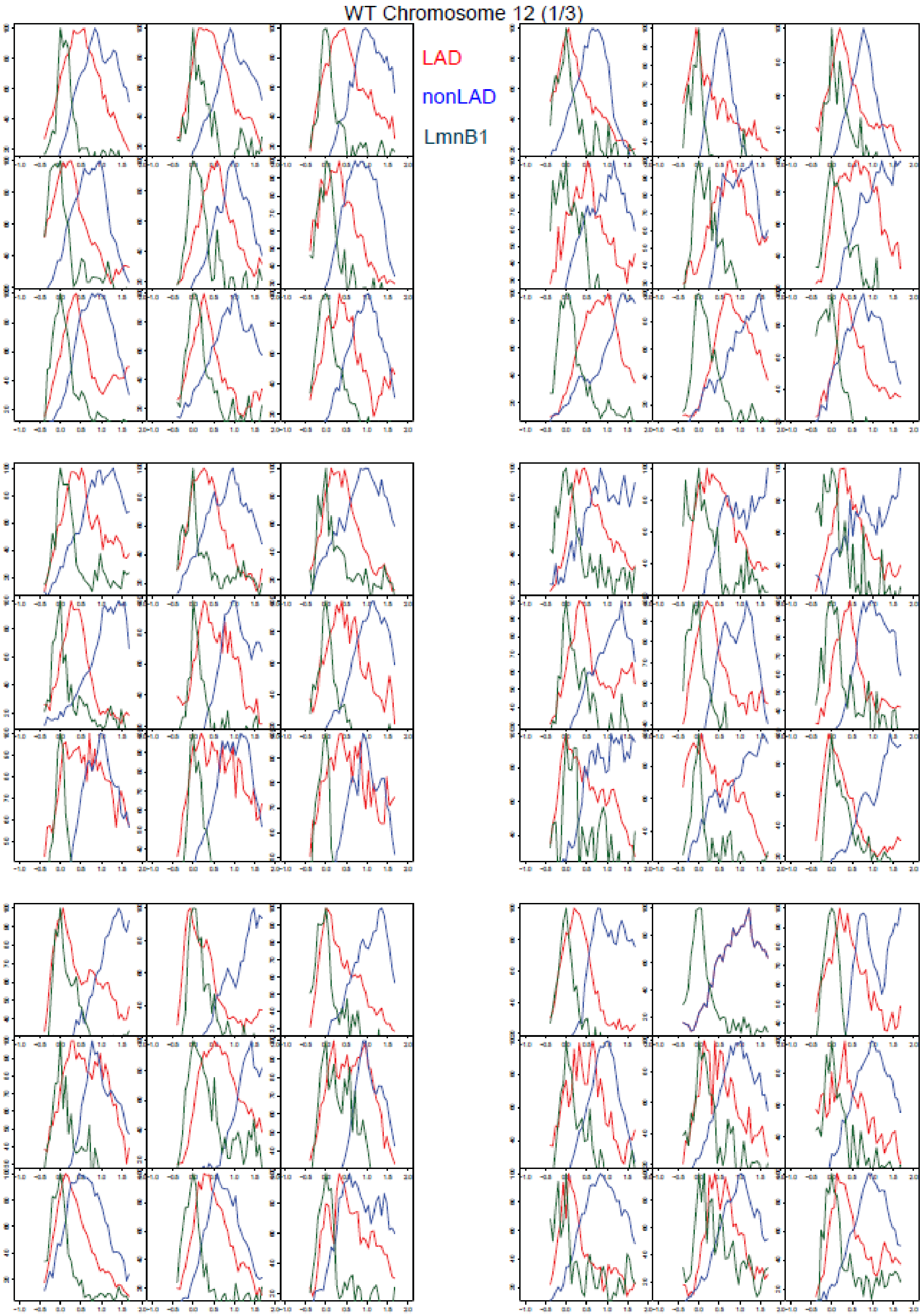
WT Chromosome 11 (2/3)



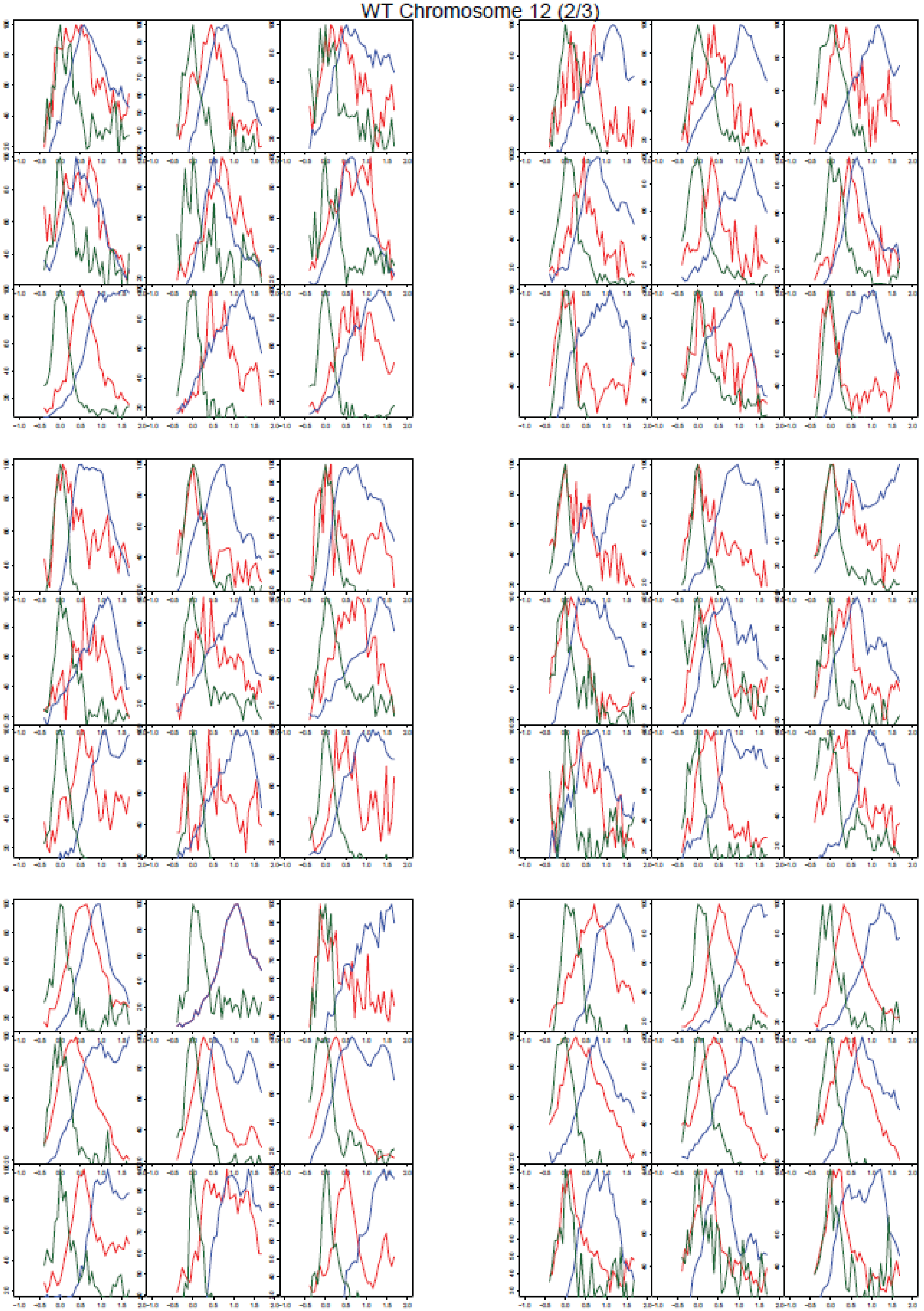
WT Chromosome 11 (3/3)



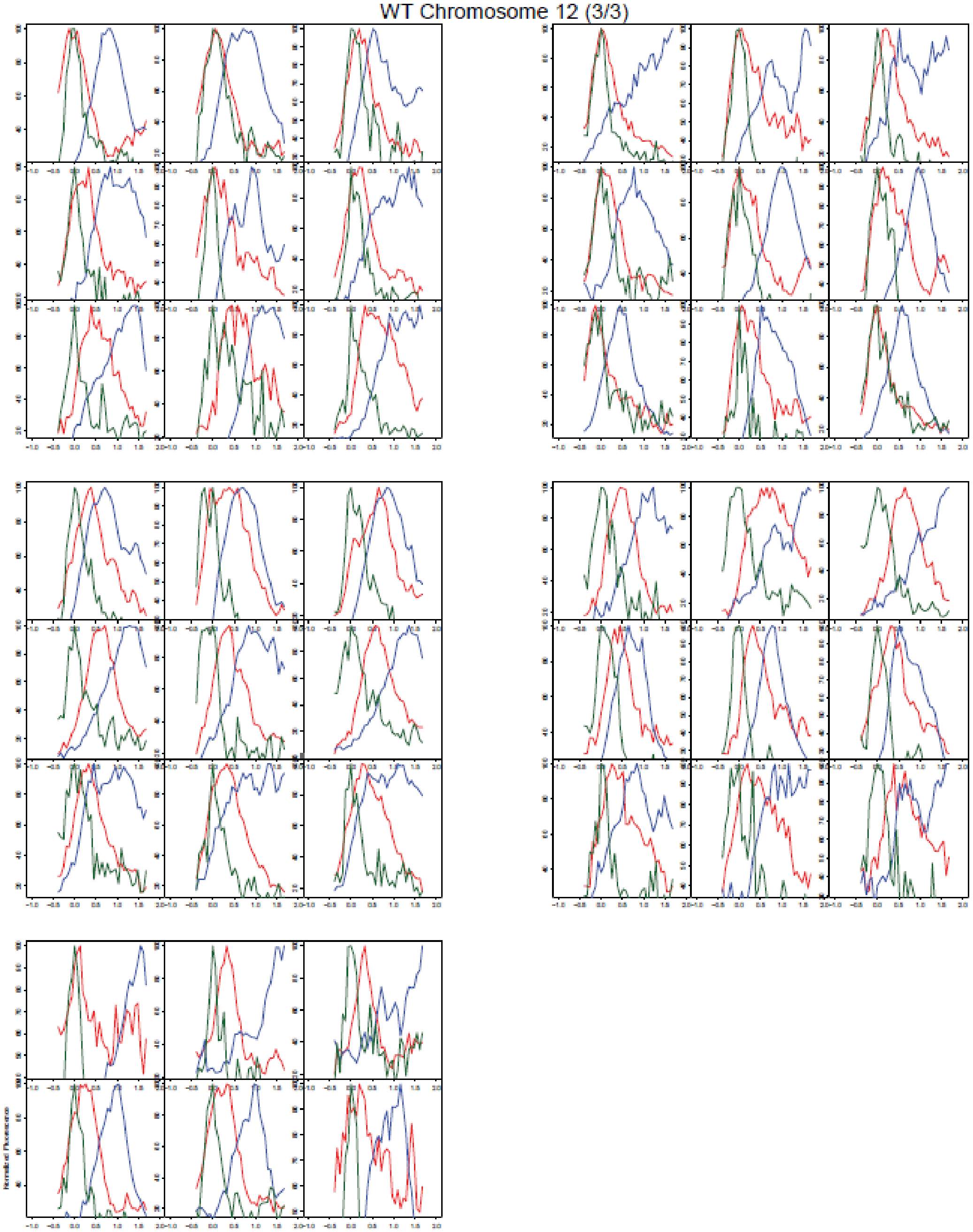
A.8.2 Chromosome 12 100x objective magnification



WT Chromosome 12 (2/3)



WT Chromosome 12 (3/3)

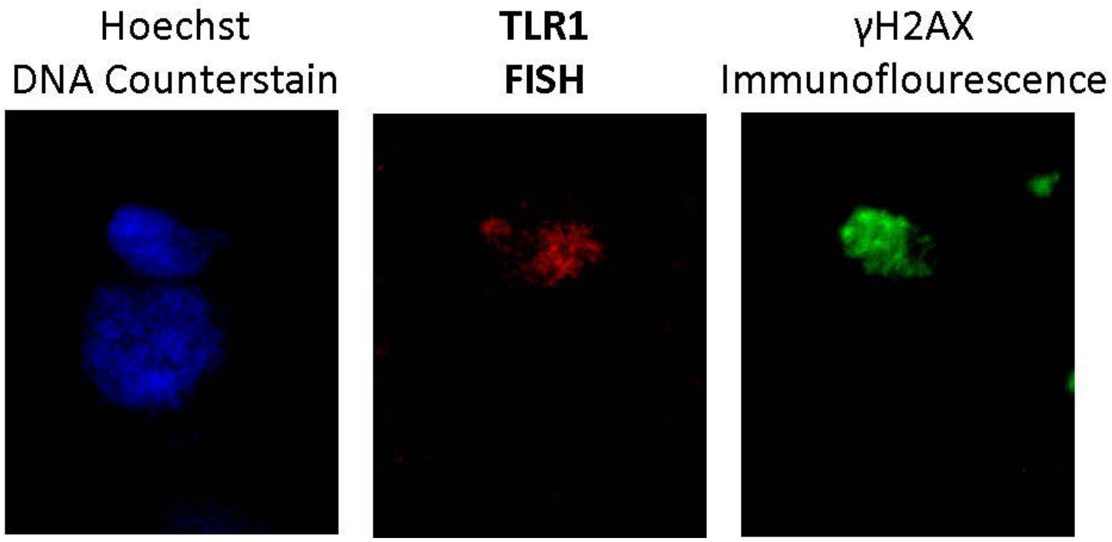


A.9 Novel protocol for Fluorescence in situ Hybridization in Tetrahymena Thermophila

Protocol to perform FISH in conjugated *Tetrahymena Thermophila* cells was developed for Papazyan R, Voronina E, Chapman JR, **Luperchio TR**, Gilbert TM, Meier E, Mackintosh SG, Shabanowitz J, Tackett AJ, Reddy KL, Coyne RS, Hunt DF, Liu Y, Taverna SD. "Methylation of histone H3K23 blocks DNA damage in pericentric heterochromatin during meiosis." *e-life. 2014 August 26.* Method was described in this publication and reprinted in part here.

Fluorescence *in situ* hybridization coupled with immunofluorescence: mating *Tetrahymena* cells conjugating between 2 and 4 hr were fixed in partial Schaudin's fixative as described (Madireddi et al., 1994) (Wenkert and Allis, 1984), and dropped on slides. DNA-immunoFISH was adapted from Reddy et al., 2008. Briefly, slides were rehydrated in PBS for 20 min, and fixed again in 1% paraformaldehyde/PBS solution for 5 min, and washed three times with PBS. Slides were then RNAse treated (100 μg/ml) for 15 min in 2× SSC at room temperature in a humidified chamber. Slides were hybridized by washing in 70% formamide/2x SSC at 76°C for 3 min, then 50% formamide/2x SSC at 76°C for 1 min, and then incubating with denatured and preannealed probe/hybridization solution (Cy5 labeled Tlr1 probe, 9 μg salmon sperm DNA, 6 μg placental DNA, 10% dextran sulfate, 50% formamide, and 2× SSC) overnight at 37°C in a humidified chamber. Probe to Tlr1 element was generated by directly labeling Tlr1 PCR product with Cy5 (Primers: Forward - TCGGATCGGATTGGATTAAC, Reverse -CCTGGAGCTTACCGTCTTTG; Aglient Genomic DNA ULS labeling kit 5190-0419). After overnight incubation, slides were washed three times in 50% formamide/2× SSC at 47°C, three times with 63°C 0.2× SSC, one time with 2× SSC, and then two times with PBS before blocking with 4%

BSA in PBS for 30 min in a humidified chamber. Slides were then incubated with primary antibody (α-γH2AX [1:100; 613402; BioLegend, San Diego, CA]) in blocking medium overnight at 4°C. Slides were washed three times with PBS/0.05% Triton X-100 and then incubated with secondary antibody in blocking medium (1:100; DyLight 488, Jackson ImmunoResearch, West Grove, PA) for 1 hr at room temperature. Post incubation, slides were washed three times with PBS + 0.05% Triton X-100, and then DNA counterstained with 1 µg/ml Hoechst. Slides were then washed, mounted with SlowFade Gold (Life Technologies).



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CURRICULUM VITAE

Education

The Johns Hopkins School of Medicine, Baltimore, MD **2016**

Ph.D. in Biological Chemistry
Department of Biological Chemistry, and Center for Epigenetics
Biochemistry, Cellular and Molecular Biology (BCMB) Program
Thesis: "The role of Lamin Associated Domains in global chromatin organization and nuclear architecture"

The Johns Hopkins University, Baltimore, MD **2008**

Bachelor of Science in Molecular and Cellular Biology
Zanvyl Krieger School of Arts and Sciences

Skills

- Microscopy techniques including 3D fluorescence in situ hybridization (FISH), immunofluorescence, in situ proximity ligation assay ISPLA
- Advanced image processing
- Tissue dissection, sample preparation and primary cell culture
- General tissue culture techniques, virus production and infection
- Molecular biology and genomics techniques including preparation of samples for ChIP, DamID, Next-Generation Sequencing
- Sequencing and microarray data management, processing, and analysis
- Bionformatics and computer-based research, including experience with online genome research tools such as NCBI database tools, UCSC Genome Browser, GALAXY
- R, PERL, HTML, JavaScript, general UNIX and LINUX commands
- Effective science communication to lay public, congressional and scientific audiences
- Large and small group facilitation, delivery of educational presentations and lectures
- Training, team building, project management
- Expertise with Microsoft Office applications including Word, Excel, Access, and PowerPoint
- Fundraising, cold-calling, phone outreach, rapport building

Experience

Graduate Researcher **2008-2016**

Advisor: Dr. Karen L. Reddy, The Johns Hopkins School of Medicine, Baltimore, MD

- Discovered a unique sub-chromosomal organization in the nucleus and discovered an unprecedented genome destabilization with a variety of epigenomic perturbations.
- Elucidated features of the relationship of epigenetics with nuclear architecture/dynamics and functional genome organization in development and disease.
- Developed genomic and microscopy techniques and tools to visualize genome wide molecular data in single cells.

- Led and assisted in translating complexities of genome, epigenome, and chromosome organization research into written and oral language understood by lay and professional audiences through journal clubs, departmental presentations, national conference talks and poster sessions, literature reviews, and contributing to laboratory grant writing and manuscripts for publication.
- Used computing tools to interpret genomic data, and produce reports for discovery, data validation, and overview of project progress.
- Prepared analysis, reports and documents for use in reporting to senior scientists that advanced genomic research, guided research project direction, long-range plans and research priorities.
- Evaluated data analysis to support basis for research decisions for projects focused on novel mechanisms for targeted genome organization and structure.
- Delivered frequent oral presentations reporting on analysis of data to senior staff, including professors, department and committee chairs, and center directors.
- Summarized key research findings and results from written scientific reports, including literature reviews focused on genome structure and organization in development and disease.
- Coordinated, supported and assisted in development and advancement of research initiatives, and production of publications on team projects, both as team leader and team member.
- Advised senior scientists on project goals, status, and projections, and facilitated peer project publication success and policy development.
- Designed, conducted, and managed independent experiments, and coordinated multiple projects.
- Supervised and mentored high school, undergraduate, and graduate students.

Public Policy Fellow **2015**
Federation of American Societies for Experimental Biology (FASEB), Office of Public Affairs, Bethesda, MD

- Organized briefings for Congressional staff on Capitol Hill on current and cutting edge biomedical research, including the microbiome, and the use of canine models in research with a focus on comparative genomics topics.
- Coordinated with other organizations, including professional scientific societies, to develop and advance the topic and scope of a Congressional briefing series.
- Assisted in translating complexities of genetic and genomic research and policy, specifically regarding the Precision Medicine Initiative, into written and oral language understood by lay and professional audiences for internal reports.
- Developed reports and educational materials, including species-specific factsheets for the public on the importance of animals in research.
- Summarized key biomedical research findings and results from written scientific reports and translated scientific information into lay language for a non-scientific audience for inclusion in publicly posted factsheets on animals in research and public notices regarding policy statements.

- Responded to a Request for Information (RFI) solicited by NIH/NCATS regarding their five-year strategic plan (NOT-TR-16-002), analyzed existing policies to identify gaps and identify policy needs.
- Contributed to discussion of analysis of the impact of legislative proposals and proposed regulations on healthcare research programs.
- Prepared briefing materials on policy issues on reproducibility in science, animals and research and other issues relating to biomedical research.
- Lobbied Congressional offices for support for biomedical research by vising with members of Congress and Congressional staff though participation in a Capitol Hill Day sponsored by the American Physiological Society.

Teaching Assistant (Graduate level course – PhD audience) **2013**
Effective Science Communication, The Johns Hopkins School of Medicine, Baltimore, MD

- Assisted trainee scientists in translating complexities of research into graphical, written, and oral language understood by lay and professional audiences.
- Prepared reports and documents to report to senior officials, including student evaluations, and grade reports.
- Assessed student progress and provide personalized student assistance.

Program Coordinator **2012- 2013**
BCMB Colloquium, The Johns Hopkins School of Medicine, Baltimore, MD

- Organized and planned a research colloquium program for graduate scientist trainees.
- Solicited speakers for cross-disciplinary sessions, coordinated judging aimed at providing feedback to presenters on accessibility of complex techniques and concepts to a diverse audience.
- Managed colloquium activities, including the budget, participation and attendance, meeting logistics, and reported on the program to senior officials.

Teaching Assistant (Graduate level course – MD audience) **2012- 2013**
Scientific Foundations of Medicine, Cellular Physiology, The Johns Hopkins School of Medicine, Baltimore, MD

- Summarized key health research findings and results from written scientific reports to facilitate group discussion in daily lectures and provide personalized student assistance in a healthcare education program.
- Prepared reports and documents to report to senior officials, including session summaries, student evaluations, and grade reports.
- Assessed student progress and provide personalized student assistance.

Undergraduate Researcher **2007- 2008**
Advisor: Dr. Andrew Hoyt, Department of Biology, The Johns Hopkins University, Baltimore, MD

- Investigated kinetochore structure and function using *Saccharomyces cerevisiae* as a model.
- Gave oral presentations to senior staff reporting on an analysis of data.

Head Course Assistant (Undergraduate level course) **2005- 2007**
Department of Computer Science, The Johns Hopkins University, Baltimore, MD

- Planed and implemented policy initiatives, including creating and revising curriculum for multiple computational platforms.
- Formulated and administered weekly lectures with multimedia supplements to facilitate learning.
- Recruited and trained course assistants for grading, lecturing, and individualized student aid.

Supervisor and Non-Profit Representative **2004 –2008**
The Johns Hopkins University Phonathon – RuffaloCODY, Baltimore, MD

- Supervised, trained, and managed a staff of over 60 Johns Hopkins University representatives raising over $9,000,000 in unrestricted capital.
- Developed exemplary communication skills, while personally raising $100,000 in total funds.
- Developed methods to evaluate the efficacy of fundraising initiatives using computing tools to interpret data on individual and overall employee performance and produce novel and innovative reports on a weekly basis.
- Utilized an electronic database to analyze employee performance and project goals.
- Developed long range plans that established policy and priorities regarding employee performance.

Publications

Wong X, **Luperchio TR**, Heydarian M, Wheelan SJ, de las Heras J, Schirmer EC, Reddy KL. LADetector: a rapid, large-domain calling algorithm that allows for accurate identification of edges and dips with both ChIP and DamID technologies, *Manuscript in preparation*

Luperchio TR. “Can Cell Lines Replace Animal Research?” Speaking of Research 2015 November 25

Luperchio TR, Halstead M, Wong X, Ach R, Pekrun K, Yamada N, Reddy KL. “Visualization of large scale genomic data uncovers the functional organization of chromosomes in single cells”. *Manuscript in preparation*

Harr JC, **Luperchio TR**, Wong X, Cohen E, Wheelan SJ, Reddy KL “Directed targeting of chromatin to the nuclear lamina is mediated by chromatin state and A-type lamins”. *JCB 2015 January 5*

Papazyan R, Voronina E, Chapman JR, **Luperchio TR**, Gilbert TM, Meier E, Mackintosh SG, Shabanowitz J, Tackett AJ, Reddy KL, Coyne RS, Hunt DF, Liu Y, Taverna SD. "Methylation of histone H3K23 blocks DNA damage in pericentric heterochromatin during meiosis." *e-life. 2014 August 26*

Wong X, **Luperchio TR**, Reddy KL. "NET gains and losses: the role of changing nuclear envelope proteomes in genome regulation." *Current Opinion Cell Biol. 2014 June 28*

Luperchio TR, Wong X, Reddy KL. "Genome regulation at the peripheral zone: lamina associated domains in development and disease." *Current Opinion Genet Dev. 2014 April 25*

Heydarian M, **Luperchio TR**, Cutler J, Mitchell CJ, Kim MS, Pandey A, Sollner-Webb B, Reddy KL "Prediction of Gene Activity in Early B Cell Development Based on an Integrative Multi-Omics Analysis." *Journal of Proteomics & Bioinformatics. 2014 February 17*

Zullo JM, Demarco IA, Piqué-Regi R, Gaffney DJ, Epstein CB, Spooner CJ, **Luperchio TR**, Bernstein BE, Pritchard JK, Reddy KL, Singh H. "DNA sequence-dependent compartmentalization and silencing of chromatin at the nuclear lamina." *Cell. 2012 June 22*

Published Abstracts

ASCB Annual Meeting 2015, 2014

Luperchio TR, Wong X, Halstead M, Ach R, Pekrun K, Yamada N, Reddy KL. “Visualization of large scale genomic data in single cells uncovers the functional organization of chromosomes”

Presentations and Recognition

Women in Cell Biology Travel Award	**2015**
Poster Presentation, ASCB	**2015**
Lecture, Genomics and Bioinformatics Symposium	**2014**
“Making and Breaking LADs: A Study of Genome Architecture”	**2014**
Poster Presentation, ASCB	**2014**
e-Poster Presentation, ASCB	**2012, 2013**
Chromatin Club	**2009**
3rd place in Poster presentation competition, BCMB Annual Retreat	
Dean’s List	**2006**
Edward J. Bloustein Distinguished Scholar	**2004**
Sons of Italy New Jersey Foundation Scholarship	**2004**

Committees and Leadership

American Society for Human Genetics DNA Day Essay Contest, *Judge*	**2015** **2015-present**
American Society for Human Genetics, *Member*	**2014-present**
Association for Women in Science, *Member*	**2014-present**
Sigma Delta Epsilon - Graduate Women in Science, *Member*	**2014-present** **2014-present**
American Association for the Advancement of Science, *Member*	**2014-2015**
American Society for Cell Biology, *Member*	
Hopkins Science Policy Advocacy Network, *Member*	
Johns Hopkins University Leadership Symposium, *Invited Participant*	**2013-2016**
BCMB Program Research Colloquium, *Program Coordinator*	**2012-2013**
BCMB Lectureship Search Committee, *Committee Member*	**2012-2013**
BCMB Program Research Colloquium, *Judge*	**2011**